TROPHIC AND SIZE SPECTRA MODELING REVEAL KEY SPECIES INTERACTIONS AND QUANTIFY COMMUNITY RECOVERY DYNAMICS WITHIN NEWFOUNDLAND AND LABRADOR FISHERIES ECOSYSTEMS

by

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Abstract

Recent efforts to shift towards ecosystem approaches to fisheries management require multi-species analyses across dynamic food webs and an understanding of trophic dynamics. My research analyzed the marine food web dynamics of Newfoundland and Labrador using stomach contents data and stable isotope ratios from fishes and invertebrates. A key facet of trophic ecology is the role a species fills in the food web. My first chapter quantified realized isotopic niches, a proxy for trophic niche, of representative dominant species using Bayesian ellipses and assess the potential competitive interactions that could prevent population recovery of groundfish species. Also essential in trophic ecology is the assessment of nutrient flow through an ecosystem. To understand the origin for the spatially varying isotopic niches, isotope mixing models were created in my second chapter to assess the strength of the interactions between all fish species and prey species and assess the key pathways of nutrient flow to the upper food web. Considering bioenergetic transfer through a system requires consideration of productivity resulting from growth and reproduction. This productivity analysis lends itself to the study of size spectra and the question of whether they may be used to assess community recovery. To do so, in my third chapter the empirical size structure I derived from the ecosystem surveys was compared to a theoretical pristine size structure derived through a combination of nitrogen stable isotopes and macroecological principles. Strong regionality was observed in isotopic signatures, with more trophic niche overlap, increased connectance and shorter food chain length in the less diverse, northern sites. Ontogenetic variation was observed in the isotopic niches and in the reconstructed diets.

These trophic considerations may contribute to the observed differential recovery rates of fish stocks, illustrating the importance of considering competition and diet composition. The interactions of recovering groundfish species and economically important invertebrate species (i.e. shrimp and snow crab) were also highlighted. Although the Newfoundland and Labrador marine ecosystems were still far from fully recovered, recovery and continued sustainability of fish communities could be facilitated through balanced harvesting (though presently mostly theoretical) to limit the damaging impacts of fishery exploitation.

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List of Abbreviations and Symbols

Abbreviation/Symbol	Definition
δ	A measurement of the stable isotope ratio determined by taking the ratio of the heavier isotope relative to the standard molecule and comparing it to a reference standard R.
$\delta^{13}C$	Stable carbon isotopic value of carbon-13 in delta notation.
$\delta^{15}N$	Stable nitrogen isotopic value of nitrogen-15 in delta notation.
λ	Inverse Simpson Index. A measure of species diversity.
ANCOVA	Analysis of Covariance. A general linear model which blends ANOVA and regression.
ANOVA	Analysis of Variance. A collection of statistical models used to analyze differences among group means.
B	Biomass Density. The amount of fish biomass in grams per square meter.
BC	Bonavista Corridor. The southern-most region in this study between the Grand Bank and the Funk Island Bank.
f	The proportion of a predator's diet prepresented by a given prey species.
FO	Frequency of Occurrence. The number of stomachs in which a given prey item is found over the total number of stomachs in a sample.
GEBCO	General Bathymetric Chart of the Oceans. An online database of publicly available bathymetry sets for the world's oceans.
HC	Hakwe Channel. The northern-most region in this study between the Hamilton Bank and the Bell Island Bank. Notable for a marine protected area.
IRI	Index of Relative Importance. A measure of relative importance of prey to the diet of a predator. Determined for each prey item by summing the percent by weight and the percent by number and multiplying that sum by the frequency of occurrence.
M	Body Mass Category. Log_2 body mass categories measured in grams.
NAFO	Northwest Atlantic Fisheries Organization. An intergovernmental organization which seeks to manage fisheries in the northwestern Atlantic Ocean. Management Divisions 2J and 3KL were established within NAFO sub-areas.
NDC	Notre Dame Channel. The intermediate region in this study Between the Bell Island Bank and the Funk Island Bank.

P	Production. The rate at which a predator produces organic compounds in grams of carbon per square meter per year.
PP	Primary Productivity. The rate at which photosynthetic organisms produce organic compounds in grams of carbon per square meter per year.
PPMR	Predator Prey Mass Ratio. The ratio of the predator body mass in grams to the prey body mass in grams.
R	Reference standard for stable isotope analysis. For nitrogen this standard is atmospheric nitrogen and for carbon Pee Dee Belemnite.
RESET	Regression Equation Specification Error Test. A test for functional form used to detect linearity vs nonlinearity.
SE	Standard Error. A measure of the statistical accuracy of an estimate determined by dividing the standard deviation by the square root of the sample size.
SIBER	Stable Isotope Bayesian Ellipses in R. R package used to create Bayesian Ellipses and associated analyses.
TL	Trophic Level. The position an organism occupies in a food chain.
‰	Parts per thousand.
%B	Percent by Biomass. The mass of a given prey item in grams over the total mass of all prey present within a sample.
%N	Percent by Numbers. The count of individuals of a given prey taxa over the count sum of all prey present within a sample.
$[C]$ or $[N]$	Carbon or nitrogen concentration of an organism.

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Chapter 1: Introduction and Overview

Fish Populations in a Changing Ecosystem

Understanding the interaction between environmental conditions and fisheries exploitation on marine communities represents one of the pressing modern issues within the field of fisheries ecology. Environmental factors which have been shown to influence fish productivity via recruitment, growth and survivability include primary production (e.g. Runge 1988, Cushing 1990, Trites et al. 1999, Mackinson et al. 2009), salinity (Mann & Drinkwater 1994, Dutil & Brander 2003, Hidalgo et al. 2015), and temperature (e.g. Pepin 1991, Pörter et al. 2001, Mieszkowska et al. 2009, Gislason et al. 2010, Rountrey et al. 2014). Primary production alone is influenced by a number of additional factors such as wind conditions (Sakshaug & Slagstad 1992, Albert et al. 2010), UV radiation (Smith & Baker 1982, Prézelin et al. 1994, Lotze et al. 2002), ocean acidification (Koch et al. 2012, Beardall et al. 2014), carbon dioxide levels (Riebesell et al. 1993, Gao et al. 2012), and nutrient availability (Barber & Chavez 1991, Cullen et al. 1992, Bonnet et al. 2008). Together these factors are thought to impact fish production and thereby fisheries yields. Whether these impacts positively or negatively impact fish populations depends not only on the factor but their interactions with the local environment (e.g. Brander 2007, Sherman et al. 2009).

In addition to environmental factors negatively influencing fish communities, exploitation has damaged marine communities. Industrialized fisheries have been shown to reduce the biomass of a community by up to 80% within the first couple of decades of exploitation (Myers & Worm 2003). This exploitation may further impact marine

communities by altering species distributions, marine ecosystem size structure and prey availability (Blanchard et al. 2003, Jennings & Collingridge 2015, Hiddink et al. 2016, Poloczanska et al. 2016). These anthropogenic impacts on the ocean often direct an ecosystem towards ecological extinction (Petersen 1903, Jackson et al. 2001). Recent estimates suggest that 93% of global fish stocks are fully exploited or overexploited (FAO 2018, Link & Watson 2019). Numerous marine ecosystems are still recovering from prior overfishing despite protective efforts (Hutchings 2000, Clark & Frid 2001, Lotze et al. 2005, Palumbi et al. 2008, Neubauer et al. 2013). Protective efforts include trawling moratoria such as those observed on the Grand Bank of Newfoundland (Schrank 2005), marine reserves such as those in New Zealand (Babcock et al. 1999, Willis et al. 2003), and international regulations such as the Common Fisheries Policy in the North Sea or the Sino-Japanese joing fishery management in the East China Sea (Golden & Garrod 1996, Keyuan 2003, Griffin 2010). One of the pressing questions within fisheries management becomes: how reversible are the impacts of fisheries? And how does environmental changes such as those induced by climate change influence potential recovery of these ecosystems?

In the northwest Atlantic Ocean environmental factors such as variation in temperatures and food availability are thought to have contributed to increased groundfish, most notably Atlantic cod (*Gadus morhua*), natural mortality rates. In combination with excess fishing, this increased mortality led to the collapse of multiple stocks and fisheries in the early 1990s (deYoung & Rose 1993, Bundy 2001, Robichaud & Rose 2004, Rose 2005). Since fisheries moratoria were established in Atlantic Canada

in the early 1990s, diverse population responses have been observed in adjacent stocks: some stocks have responded positively to fishery closures while other stocks have not. For example, Atlantic cod stocks in southern Newfoundland (Northwest Atlantic Fishery Organization Division 3Ps) exhibited historical population growth rates with no unexplained mortality or reduced body condition (Rose 2003, Fisheries Resource Conservation Council 2011, DFO 2019a), while those on the adjacent northern Grand Bank (3L) and the continental shelf north to Labrador (3K & 2J) have exhibited some population growth but not full recovery (Lilly et al. 2008, DFO 2018a). The stocks in these regions have not follow the trends predicted by traditional single-species models. Therefore, new approaches are required to assess the dynamics of populations and assemblages in a wider ecosystem context that includes environmental drivers and/or species interactions that vary spatially which have generally not been included in single-species analyses (Bavington 2010, DFO 2018a, Rose & Walters 2019).

Within Newfoundland and Labrador fisheries ecosystems, spatial and abundance changes have occurred in many fished and non-fished species (Gomes et al. 1995, Windle et al. 2012). For example, the Atlantic cod offshore spawning stock biomass was estimated at 1.6 million t in 1962 but had declined to approximately 22,000 t by 1992 (e.g. Hutchings & Myers 1994, Atkinson et al. 1997, Rose 2007, DFO 2018a). At the same time, increases in northern shrimp (*Pandalus borealis*; Lilly et al. 2000, Parsons 2007, DFO 2018b) and snow crab biomasses (*Chionoecetes opilio;* Dawe et al. 2012, Mullowney et al. 2012) were observed. With the decline of groundfish populations, a regime shift from a groundfish dominated community to an invertebrate dominated

community was observed (Lilly et al. 2000, Windle et al. 2012, Shrank 2013). As a result of this expansion of shrimp and crab biomasses, new fisheries emerged to take advantage of these resources. Recent catches (2017) of shrimp of approximately 87,300 t within Newfoundland, were markedly increased from 21,735 t in 1991, while crab catches at approximately 25,000 t, are up from 16,093 t in 1992 (Newfoundland Statistics Agency 1994, Lilly et al. 2000, Davis & Korneski 2012, DFO 2018b, Mullowney et al. 2019). It should also be noted that both shrimp and crab populations are presently in decline, with shrimp catches having peaked in 2008/09 at 85.725 t for the region (DFO 2018b) and crab catches peaking in 2009 at 53,500 t (Mullowney et al. 2014, DFO 2017).

Recovering Groundfish Species

The potential for recovery of these groundfish, notably Atlantic cod, stocks has received substantial attention in Newfoundland and Labrador (e.g. Hutchings & Rangeley 2011, Schrank & Roy 2013, Rose & Rowe 2015), raising the pressing question: Can these populations recover? Several changes may continue to negatively affect recovering groundfish populations. Firstly, increased predation from seal populations (harp [*Phoca groenlandica*], hooded [*Cystophora cristata*], grey [*Halichoerus grypus*], harbor [*Phoca vitulina*], ringed [*Phoca hispida*], and bearded [*Erignathus barbatus*] seals) has been proposed as a limiting factor resulting from increased seal population sizes (Steele et al. 1992, Stenson et al 1997, Shelton & Healey 1999, Bundy 2001, Bundy & Fanning 2005). This hypothesis, however, has been questioned by recent research demonstrating that low food quality is more of a driving factor preventing groundfish recovery than seal

predation (Buren et al. 2014). Previous work in this region has indicated that shrimp, crab, and capelin make up a large portion of the Atlantic cod diet (e.g. Methven & Piatt 1989, Lilly et al. 2000, Krumsick & Rose 2012). Since the collapse, capelin have experienced a southward distribution and decline in abundance in the Newfoundland and Labrador region (Lilly 1994, Carscadden & Nakashima 1997, Rose & O'Driscoll 2002, Murphy et al. 2018) while crab and shrimp have increased in abundance yet are exploited by present fishing activities (Lilly et al. 2000, Worm & Myers 2003, Davis & Korneski 2012, DFO 2018b, Mullowney et al. 2019). It is therefore likely that cod's interactions with prey species have changed over time to accommodate these changes in their environment such that relatively lower quality prey such as shrimp and crab are consumed more frequently at the cost of reducing the high energy value capelin consumption. Furthermore, since the multiple groundfish stock collapses there have been life history changes in numerous groundfish species including reduced growth rates, earlier maturation and poor condition which futher hinder recovery (Olsen et al. 2004, Baulier et al. 2006, Shelton et al. 2006, Fudge & Rose 2008k, Lilly et al. 2008). With these changes in predation and life history characteristics in addition to human exploitation of the important prey species, the question arises of can the ecosystem naturally revert to its pre-1990 state? Alternatively, should we anticipate that the ecosystem can persist in a new state of functionality as a permanent regime shift (i.e. a persistent change in the structure and function of an ecosystem)?

Although Atlantic cod receives the most attention from researchers, other groundfish species have shown comparable changes to their life histories and their role within the

food web in response to prior overexploitation. Seals consume a variety of groundfish species, notably American plaice (*Hippoglossoides platessoides*) and Greenland halibut (*Reinhardtius hippoglossoides*), as well as pelagic species, namely capelin, often in greater quantities than Atlantic cod (Lawson et al. 1998, Hammill & Stenson 2000). Evidence of comparable fisheries-induced evolution, including ages and sizes at maturity, as well as changes in size spectra and condition have also been documented for a variety of local groundfish species around the time of the moratoria in the early 1990s (e.g. Bowering 1989, Bowering & Brodie 1991, Haedrich & Barnes 1997, Barot et al. 2005, Hutchings & Baum 2005, Halliday & Pinhorn 2009). Though recent attention has been in regards to Atlantic cod consumption of crab (Neis 1992, Davis 2015, Greenham 2019), a number of other fish species, including thorny skate (*Amblyraja radiata)* and American plaice, are also known to consume crab and shrimp with regular frequency in this region (e.g. Templeman 1982, Albikovskaya & Gerasimova 1993, Hutchings 2002, Link et al. 2002, Dwyer et al. 2010). Atlantic cod are therefore not the only species within the ecosystem known to consume these economically important species and thus there becomes potential competition for the same prey resources with other fish species as well as with fisheries.

Socio-economic Considerations for Population Recovery

In addition to changes in biological factors and fishing effort for numerous species, socio-economic considerations have also changed with time. Following the collapse of groundfish stocks, government policies supported the growth of the shellfish industry

including investing $140 million into processing plant construction and improving harvesting capacity (Hamilton & Butler 2001). Currently shrimp prices are $1.65 per pound and snow crab $5.22 per pound, while grade A Atlantic cod is $0.63 per pound (FFAW 2019). In contrast, in 1991, before the moratorium was declared, the price of shrimp was $0.92 per pound, snow crab $0.61 per pound, and Atlantic cod $0.32 per pound (Newfoundland Statistics Agency 1994). Although the price per pound has increased for all commercially exploited species, the clear species of economic importance are the crustaceans and molluscs whose value have increased four- to five-fold (Newfoundland Statistics Agency 1994, DFO 2019b). In contrast, groundfish have only increased threefold primarily driven by the expansion of the Greenland halibut (*Reinhardtius hippoglossoides*) fishery. These price differences, combined with large-scale changes towards the dominance of shellfish in Newfoundland fisheries, have led to shifts in overall fisheries values. Shellfish now represent 84% of the landed value of capture fisheries resources in Newfoundland and Labrador while prior to the groundfish stock collapses it only represented 34%. Conversely, groundfish now represent 13% of the landed value while they previously represented approximately 58% (Mather 2013, DFO 2019b). With capital having migrated between marine resource commodities, harvesters have expressed anxiety at the potential shift of the fishery back towards a less valuable resource (Davis, 2014). We are thus observing in this region a divide between the advocates of Atlantic cod recovery and the dissenters who prefer the status quo ("cod is God" vs "sod the cod"; see Gary et al. 2008, Davies & Rangeley 2010).

Impacts on predator populations may have ecosystem-wide top-down effects (Hairston et al. 1960, Oksanen et al. 1981, Carpenter & Kitchell 1988). This is especially important within the waters of Newfoundland and Labrador, where Atlantic cod and other predatory fishes consume species that yield the majority of high-value fisheries landings (including crab and shrimp) (Worm & Myers 2003, Windle et al. 2012, Schrank & Roy 2013, Mullowney et al. 2014). Therefore, analyzing food web interactions and parameterizing food web models involving these key species are critical to understanding and predicting potential trade-offs in fisheries yields that may be largely driven by rates of predation. Such analyses and model construction are the foundations of my PhD research.

The Stable Isotope Approach to Community Ecology

Modern single-species models have not been able to accurately predict the behaviour of commercially important species due to a lack of consideration of effects on non-target species and trophic interactions (Pikitch et al. 2004, Worm et al. 2009, Hillborn 2011). Therefore, a shift towards a multispecies ecosystem-based approach to fisheries management presents as a means to observe and assess fisheries sustainability (Link 2010). While this approach is not necessarily new (in fact it has traditionally been used for millennia by native Oceania fishermen [Johannes 1982]), single-species population assessment models were historically favored for their relative simplicity, reduced cost, and being less demanding of data (Katsanevakis et al. 2011). In order to shift towards the more complex community based fisheries management and eventually ecosystem based

management with the inclusion of abiotic factors, research is required to understand a target species' role within the ecosystem, how its dynamics affect local communities, and how a species is affected by changes in environmental conditions.

Knowledge of diet and consumption by dominant predatory species is a key input to ecosystem approaches to fisheries management as such species interactions are one of the main factors regulating fish populations (Hollowed et al. 2000, Pitcher & Heymans 2002, Link & Garrison 2002a, Bundy & Fanning 2005, Naiman & Latterell 2005). Stomach content data have historically been used extensively to describe trophic dynamics through time (e.g. Livingston 1989, Hanson & Chouinard 2002, Pinnegar et al. 2015, Buckley et al. 2016). Stable isotope analysis provides a complement to stomach content analysis. While stomach contents may provide a snapshot of the exact species consumed at a given moment, stable isotopes provide a means to resolve food webs on the scale of months (Fry 1988, Lorrain et al. 2002, MacNeil et al. 2006, Olson et al. 2010). For example, stable nitrogen isotope signatures are typically enriched among consumers with enrichment at a single feeding instance by approximately 3 ‰ for fish species. This facilitates approximation of trophic level at which the animal has fed (Minagawa & Wada 1984, Ambrose & DeNiro 1986, Vander Zanden et al. 1997). This enrichment results from the preferential removal of the lighter amine groups during deamination (Macko et al. 1987).

Photosynthesis also generates distinct carbon signatures between phytoplankton and inshore benthic carbon sources, allowing for dietary analysis to determine benthic or pelagic origin of prey (DeNiro & Epstein 1978, Petersen & Fry 1987, Hobson 1987,

France 1995, Hecky & Hesslein 1995). The exact cause of this variation is largely uncertain (Kelly 2000), but a number of factors may contribute including whether the carbon source fixes carbon dioxide or bicarbonate (Maberly et al. 1992), whether the plant uses the C3 or C4 pathway of carbon fixation (O'Leary 1981, Reinfelder et al. 2000), slower diffusion of carbon dioxide in water counteracting enzymatic discrimination (O'Leary 1988), and cell size and geometry (Popp et al. 1998). However, given the depths which were sampled in the presented study (between 285 and 425 m), benthic primary production is less likely to be driving the benthic food web. Instead, it is detrital matter that would be the base of the benthic food web, which is anticipated to have a high carbon isotopic signature as well as a mid-range nitrogen signature (Schlacher & Wooldridge 1996, Wooler et al. 2003, Tewfik et al. 2005). Carbon has also been determined to exhibit little to no fractionation, with measured fractionation coefficients typically ranging between 0 and 1 ‰ for muscle tissue (DeNiro & Epstein 1977, Macko et al. 1982, Tieszen et al. 1983, Fry & Sherr 1984, Pinnegar & Polunin 1999). Used in combination, these nitrogen and carbon isotopic values characterize the isotopic niche that individuals occupy within the community; the isotopic niche is thought to act as a proxy for the trophic niche (Bearhop et al. 2004, Newsome et al. 2007).

Scope of the Present Research

This project focuses on the northeast shelf of Newfoundland and southern shelf of Labrador contained within NAFO subdivisions 2J and 3KL, representing the

management for the formerly dominant "northern cod" stock of Atlantic cod (Templeman 1979, Rose et al. 2000, Smedbol & Wroblewski 2002). The Atlantic cod in these subdivisions are managed as a single stock without consideration of spatial variation in their interactions with other species. To address this potential limitation, instead of centering this study around management units, I focused on a more biologically relevant spatial resolution: the three major offshore Atlantic cod migration pathways within this region known as the Hawke Channel, the Notre Dame Channel, and the Bonavista Corridor (Rose 1993; Fig. 1.1). These corridors represent areas where the colder waters of the Labrador Current are undercut by the relatively warmer waters of the north-west Atlantic waters (Colbourne et al. 2013). The bottom substrate is dominated by sands, clay, and ground moraine (Fillon 1976, Warren 1976, Mullowney et al. 2012). The northern-most region, the Hawke Channel, is characterized by low species diversity, low growth rates, and high mortality reported for multiple groundfish species (Colbourne et al. 2013, Anderson & Rose 2000). The Hawke Channel was once considered an important offshore spawning location for numerous groundfish including Atlantic cod and American plaice (Fitzpatrick & Miller 1979, Templeman 1981, Hutchings et al. 1994). In 2003 this region was closed to trawling and other bottom-impact fisheries following concerns for local Atlantic cod and snow crab (*Chionoecetes opilio*) populations (Fisheries Resource Conservation Council 2001, Kincaid & Rose 2014). The declines in Atlantic cod also co-occurred with increases in shrimp biomass (Lilly et al. 2000). The southern-most region, the Bonavista Corridor, is the most biodiverse of the three regions. Atlantic cod were observed to concentrate in this region as the stock

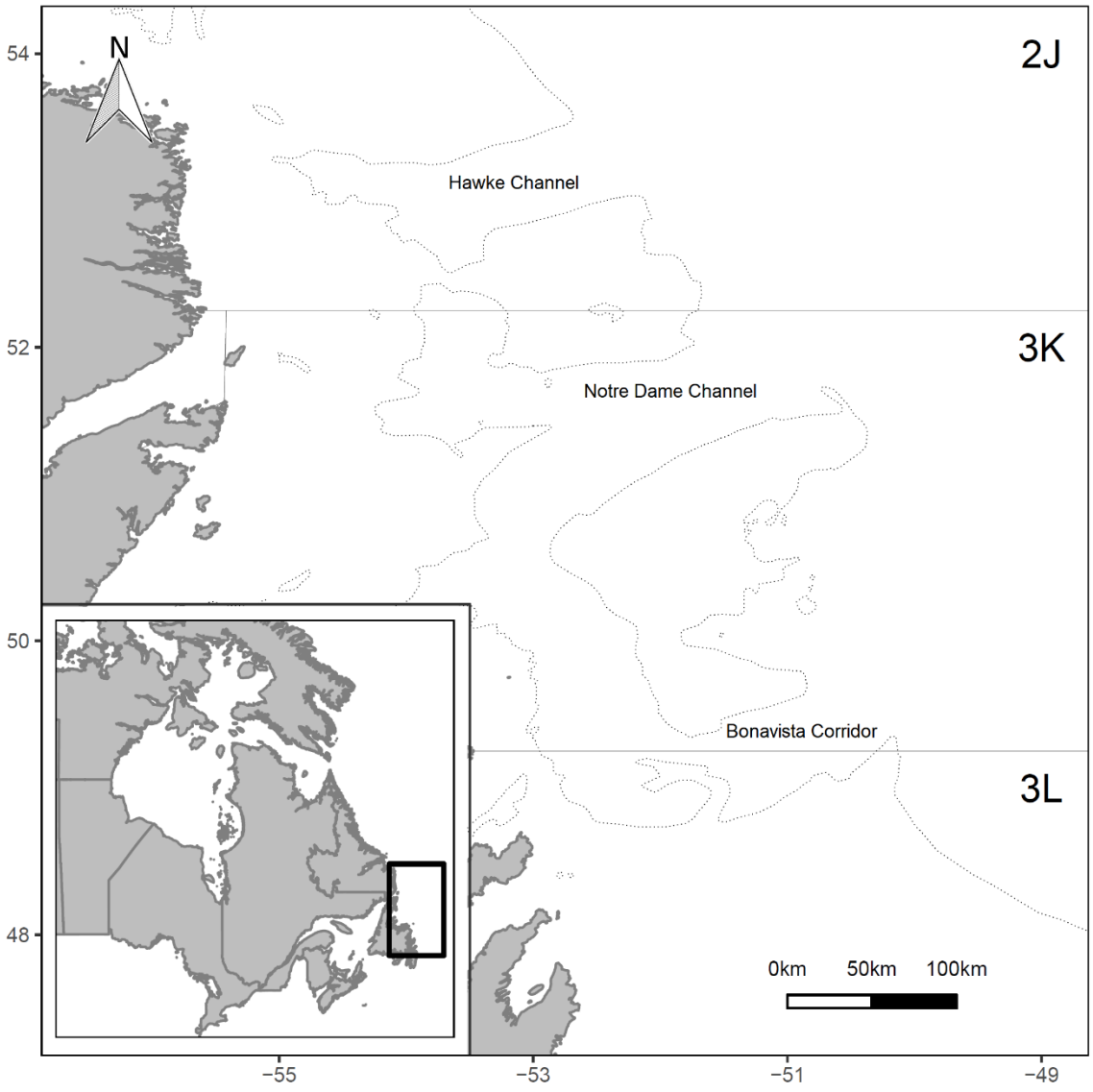

Fig. 1.1 Map of the Newfoundland and Labrador shelf, with NAFO regions indicated, that served as the study area for this research. Three channels, which serve as warm-water cod migration corridors and the basis for division of this region for these studies, are noted. The dotted line represents the 300 m depth contour of the Newfoundland and Labrador Shelf.

declined (DeYoung & Rose 1993, Rose & Kulka 1999) and has been proposed to be a key region for the recovery of the northern cod stock complex (Rose & Rowe 2018).

The organisms in the shelf communities analyzed in this study live in a complex dynamic ecosystem (Levin 1998, Pedersen et al. 2017). The shift towards an ecosystem approach towards fisheries management does not require a complete understanding of all aspects of the ecosystem nor every anthropogenic impact, but expanding our understanding on the impacts of our actions on multiple fish communities will help to limit ecosystem damage (Rice 2005). Therefore, understanding what the future holds for these communities depends, in part, on further understanding of their present structure and dynamics. Many studies have focused on temporal changes observed within recovering ecosystems (i.e. Pedersen et al. 2017, Moyes & Magurran 2018). The present research utilizes this technique by highlighting the spatial changes observed in trophic structure.

One of the ways in which an organism will indirectly interact with their surrounding ecosystem is through potential competitive interactions. A trophic niche is a subset of the ecological niche, defined as an animal's place within the biotic environment (Elton 1927) or an n-dimensional hypervolume of environmental resources (Hutchinson 1957), and addresses the overall role which a species plays within the ecosystem, specifically in regards to how they respond to resources and competitors (Leibold 1995). This trophic niche can be approximated using carbon and nitrogen stable isotopes (Bearhop et al. 2004). This isotopic niche is not exactly the same as the trophic niche as a number of factors will cause additional variation in the former such as variable isotopic fractionation and tissue turnover rates (Jackson et al. 2011). The two niches, however, are tightly correlated and as such are still useful for trophic ecology. Given the importance of

trophic niches, my first chapter estimates the core isotopic niche and a variety of Layman metrics (Layman et al. 2007) to analyze the relative positions of seven abundant fish species within isotope space and quantify niche overlap and potential competition. Bayesian ellipses, a representation of standard deviation in bivariate space such as isotope biplots, have been used with stable isotope data to determine these core isotopic niches (Newsome et al. 2007, Jackson et al. 2011). In theory, this area of biplot space encompassed by the calculated ellipse will contain the majority of the individuals and as such describe the foraging behavior of that group. I then analyze the "roles" filled by these species within size classes to highlight ontogenetic variation across the three regions to highlight how these roles change among varying diet and ecosystem diversities. This chapter reveals the importance of size-based analyses in explaining the role the organisms fill within the ecosystem. It also provides insights into the potential role of competition in explaining slow groundfish population recovery rates, a mechanism proposed as a reason for the lack of Atlantic cod recovery in other regions (Bundy & Fanning 2005).

Analyzing the isotopic niche that species fill, however, is not sufficient to determine the trophic dynamics and predatory interactions occuring within a given ecosystem. Carbon and nitrogen stable isotopes can provide further insights through the parameterization of isotope mixing models where isotopic signatures are used to determine approximate dietary contributions for a given predator (Schwarcz 1991, Phillips 2001). Exact proportions of prey based on isotopic signatures may be determined in cases where three or fewer prey sources are present, otherwise these proportions are

determined though iterative determination of contribution combinations with input likelihoods based on stomach content priors (Stock et al. 2018). My second chapter therefore applies isotope mixing models to data derived from Newfoundland and Labrador shelf regions to quantify trophic interactions in order to better understand energy flow and determine key prey species. In these analyses, considering the trophic interactions of a few predators is insufficient to characterize ecosystem functioning so I present results on a wide variety of predators and prey informed both by isotopic signatures and stomach contents. Due to potential regional variation in the role organisms fill within the ecosystem, I investigated which species were important to the community as a whole. I also focused more closely on three economically important species to assess main channels of energy flow with particular interest in their interactions with shrimp and crab. The relative importance of the pelagic and benthic communities was also assessed to emphasize how the magnitude of the two basic food chain pathways will vary spatially.

Given the expectation that understanding species interactions is required to inform any shift towards ecosystem-based fisheries management, fisheries ecology also requires means of assessing community recovery from prior overexploitation. Using a combination of predator-prey mass ratios derived from stable isotope values relative to a reference species, primary productivity estimates obtained from published literature, and a range of trophic efficiencies (Kerr 1974, Andersen et al. 2009), my third research chapter derived an estimate of a hypothetical pristine size structure for three Newfoundland and Labrador fisheries ecosystems, based on methods first described by

Jennings & Blanchard (2004). This chapter provides an indication of the community carrying capacity and, using empirically derived size spectra, determines the distance from the hypothetical pristine state. The derived biomass densities serve as an overall indicator of how far the ecosystem is from a truly recovered state despite fishing moratoria. The descending slope of the empirical biomass spectra relative to theoretical ones also provide an indicator of overall community health. Traditionally, reference points have been set using historical biomass estimates determined during time periods that are thought to represent a recovered community. However, these time periods are either based during times when strong fishing pressures had already impacted the community (Pedersen et al. 2017) or are based on time periods when fishing was less intensive but was based purely on reported catch data rather than systematic population estimates (Rosenberg et al. 2005). The theoretical spectra in this chapter were generated in the spirit of using biological characteristics to assess fish productivity and hypothetical population size (e.g. Myers et al. 2001) and thus provides a new way of assessing these reference points by determining what could hypothetically exist in the absence of fishing. Given the development of this ecosystem indicator, future scientists and managers could use this technique to derive ecosystem-level targets for fisheries ecosystem management.

In summary, my dissertation research applies and extends knowledge of stable isotope ecology to address modern concerns related to population and ecosystem dynamics within the Newfoundland and Labrador region. Through our assessment of essentially "who eats whom," we are able to study nutrient flow through the system and identify key species within the food web. Furthermore, the study of competitive

interactions and food web complexity contribute to our understanding of factors facilitating (or hindering) the recovery of fish communities. By assessing the characteristics of the community size structure, we can add new information with which managers can make recommendations to facilitate community recovery. However, body size is not the only consideration when assessing recovery. Interspecies relationships, such as trophic relationships and competition, are required in order to prevent the new generation of management procedures from causing even wider damage to these fish communities. While target fish populations are naturally the focus of any management recommendations, it is important to consider the role filled by such target species relative to the community as a whole. Though it will likely take decades (Fung et al. 2013), with cautious management and multi-species community-level considerations, community recovery as well as individual stock recovery to productive and sustainable levels should be possible.

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Co-authorship Statement

I am the primary author of all three research papers in this thesis. This work concentrated on utilizing biological samples obtained during ecosystem surveys as part of research programs of the Centre for Fisheries Ecosystems Research (CFER). All analyses were conducted with input from Dr. Jonathan A. D. Fisher. Furthermore, I conducted a substantial amount of the laboratory work presented in this thesis to derive stomach contents quantities, archive, and prepare stale isotope samples. Finally, I conceived and wrote all manuscripts with generous amounts of analytical and editorial comments from Dr. Jonathan A.D. Fisher, who co-authors all three manuscripts produced from this thesis.

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Chapter 2: Spatial and ontogenetic variation in isotopic niche among recovering fish communities revealed by Bayesian modeling.

Abstract

Exploitation and changing ocean conditions have resulted in altered species interactions and varied population dynamics within marine fish communities off northeast Newfoundland and southern Labrador, Canada. To understand contemporary species interactions, I quantified the isotopic niches, niche overlap, and ontogenetic niche change among seven dominant fish species using stable isotope analyses. Analyses used fishes from three regions differing in fish and prey diversities. Differences in fish and diet composition diversity among regions were found using Simpson's inverse diversity index. The regions of lowest diversities had higher instances of niche overlap and higher percentage of niche overlap area. The region of highest diversity had the widest spread of niches with greater distances from the community centroid. Ontogenetic shifts were observed such that larger individuals shifted towards the community centroid with the exception of Atlantic cod. Atlantic cod in particular was found to consistently be the top predator of the analyzed species. Our results reveal: (a) overlap in isotopic niches and spread within niche space was correlated with fish and diet diversity; (b) ontogenetic shifts are important when considering a species' niche and quantifying spatial variation in community niche profiles.

Introduction

Knowledge of diet and consumption by dominant predatory species is a key input to ecosystem approaches to fisheries management as species interactions are one of the main factors regulating fish populations (Hallowed et al. 2000, Link & Garrison 2002, Bundy & Fanning 2005, Naiman & Latterell 2005, Lilly 2008). In fisheries ecosystems of Newfoundland and Labrador, since the collapse of groundfish stocks in the early 1990s (Lilly 2008), numerous changes have been observed including rising ocean temperatures (Rice 2002, Colbourne et al. 2016), a southward shift in Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) distributions (deYoung & Rose 1993, Frank et al. 1996, Rose & O'Driscoll 2002), and observed declines in Atlantic cod stocks followed by increases in snow crab (*Chionocetes opilio*) and northern shrimp (*Pandalus* sp.) populations (Lilly et al 2000, Parsons & Lear 2001, Rose 2005, Windle et al 2012, Pedersen et al 2017). Therefore quantifying spatio-temporal variation in feeding interactions and trophic structure studies is required to understand ecosystem functioning and predict future changes within this region.

The trophic niche is an essential component of a species' ecological niche resulting from predatory and competitive interactions (Leibold 1995). Trophic niches often vary throughout ontogeny as, for example, increased gape size allows for increased prey breadth (Werner & Gilliam 1984, Woodward & Hildrew 2002). In many cases body size, rather than species identity, predicts trophic position (Arim et al. 2009, Romanuk et al. 2010). Stable isotope analyses have been proposed as a means to describe the trophic niche of species and communities by representing isotope data in multivariate space.

Such portrayals are comparable to the n-dimensional space of an ecological niche (Bearhop et al. 2004, Newsome et al. 2007). However, the isotopic niche includes a combination of biotic and abiotic processes and thus is not the same as the trophic niche which result from the trophic interactions of an organism (Newsome et al. 2007, Jackson et al. 2011).The two measures are correlated as consumer-resource interactions are often a primary driver of isotopic niche (Bearhop et al. 2004, Araújo et al. 2007)

While stomach contents analyses have historically been used to describe diets, stable isotope analysis provides an alternative means of assessing energy flow through an ecosystem that integrates diet data over longer periods (Fry 1988, Lorrain et al. 2002). The stable nitrogen isotope signature ($\delta^{15}N$) typically becomes enriched by 3.4 ‰ for fish species with each consumption due to preferential removal of lighter amine groups during deamination, allowing for approximation of tophic level (Macko et al. 1982, Minagawa & Wada 1984, Vander Zanden et al. 1997). The stable carbon isotope signature ($\delta^{13}C$) provides an indication of the initial carbon source (pelagic or benthic in origin) and enriches at less than 1 ‰ with fractionation frequently considered negligible (DeNiro & Epstein 1978, Hecky & Hesslein 1995, Vander Zanden & Rassmussen 2001). Four metrics relevant to quantification of community trophic structure using stable isotopes are presented below (Layman et al. 2007, Jackson et al 2011): Bayesian ellipses overlap, mean distance to centroid, mean distance to nearest neighbour, and standard deviation of distance to nearest neighbour. These metrics, in addition to providing details on trophic interactions, provide the foundation from which more complex food web

dynamics models may be constructed (e.g. Abrantes et al. 2013, Marchese et al. 2014, Albo-Puigserver et al. 2016).

The coastal shelf ecosystems of Newfoundland and Labrador are considered recovering fish communities following overexploitation by fisheries and changing climate and ecosystem conditions (Rice 2002, Buren et al. 2014, Pedersen et al. 2015). The recovery dynamics, however, appear to vary among regions partially due to food limitations in the northern regions (Lilly 1994, Rose & O'Driscoll 2002, Mullowney & Rose 2014). This requires understanding feeding interactions within recovering fish communities and characterizing spatial differences among regions.

Towards this end, we use the four previously mentioned metrics of isotopic niche to analyze community trophic structure in recovering marine ecosystems. The specific objectives of this study are to: (a) determine the influence of species richness and diversity (both fish communities and their prey) on the community trophic structure among regions, and (b) assess the impact of ontogenetic variation on isotopic niche metrics.

Materials & Methods

Study Area

The study was conducted as part of ecosystem surveys by the Center for Fisheries Ecosystems Research (CFER) aboard the RV Celtic Explorer in May 2013 and 2015 on the offshore shelves from southern Labrador and eastern Newfoundland, corresponding to Northwest Atlantic Fishery Organization (NAFO) subdivisions 2J and 3KL (Fig 2.1;

for survey details, see Rose & Rowe 2015). These surveys were conducted in accordance with the Fishery (General) Regulations of Canada. As per section 52, experimental licenses were obtained from Fisheries and Oceans Canada (license numbers NL-1596-13 and NL-2927-15). The subdivisions 2J and 3KL together represent the management unit for the 'northern cod' stock of Atlantic cod (*Gadus morhua*). This region is dominated by the southward Labrador Current flowing along the shelf with sea surface temperatures steadily increasing with decreasing latitude (Petrie & Anderson 1983, Mason et al. 1999, Han et al. 2008). Three major channels in these regions had previously been identified as important for onshore-offshore cod migration: the Hawke Channel, the Notre Dame Channel, and the Bonavista Corridor (Rose 1993). Given their potential importance, these trenches served as the focal regions for sampling cod and all other fish species within this study.

In both years a number of sets, defined as the catch obtained from a single trawl, were done in all three regions, though the Bonavista Corridor was more extensively surveyed. The trawl data for the fish species relative biomass composition were collected in May 2013 using a Campelen 1800 trawl (Table 2.1; Fig 2.1). While other trawl gear types were also used during this survey, the Campelen 1800 trawl sets from 2013 were chosen to represent the catch data as it was the only gear deployed in all three regions, allowing for regional comparisons. Samples for isotope analysis were collected during May, 2015, utilizing a combination of Campelen 1800 and mid-water trawls (Table 2.2; Fig 2.1). The variety of gear used for the opportunistic sampling of stomachs and samples for isotope

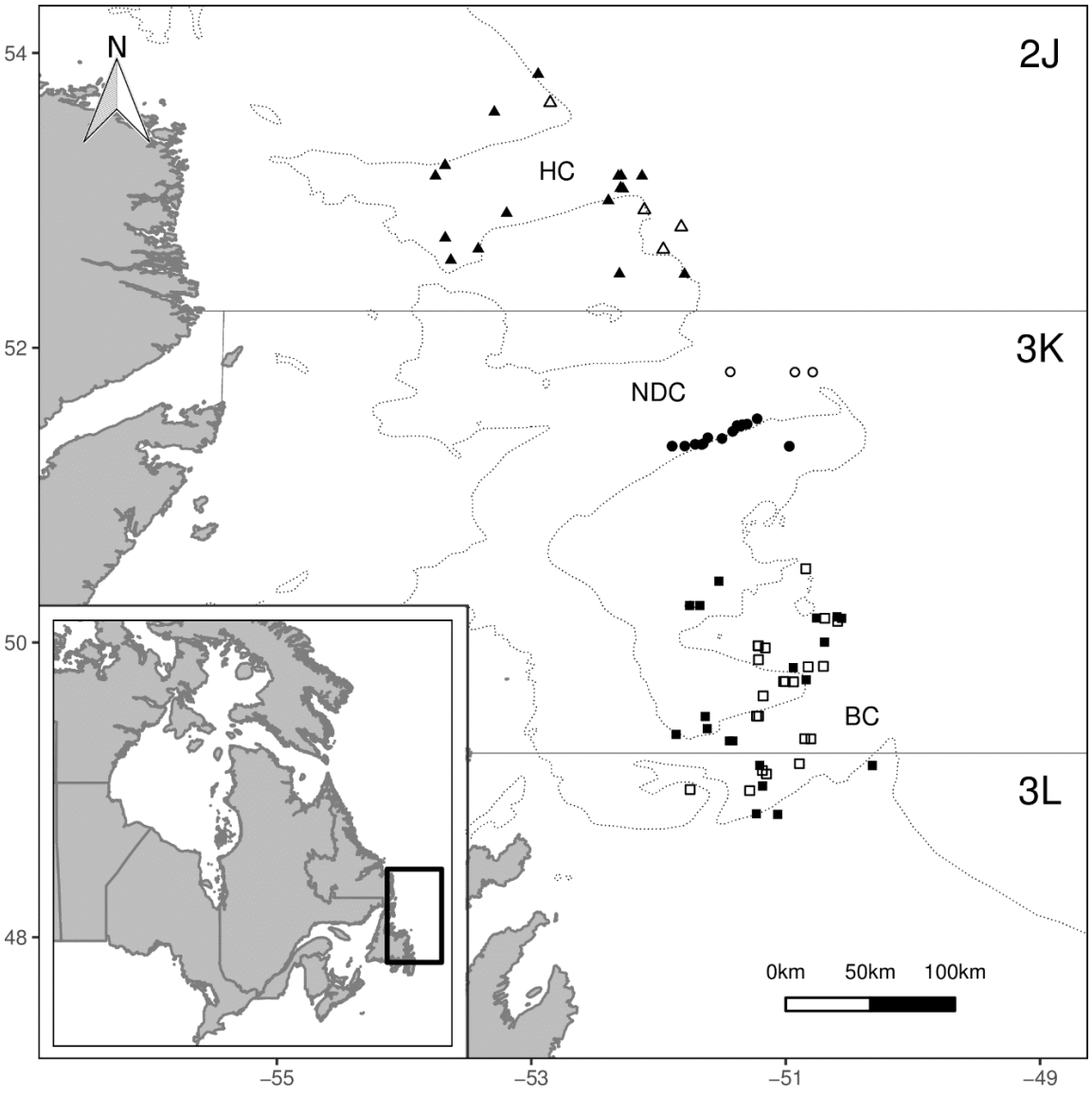


Fig 2.1 Map of Newfoundland and southern Labrador with sampling locations. The sampling locations are indicated for the 2013 (open symbols) and 2015 (closed symbols) locations within the Hawke Channel (HC, triangles), Notre Dame Channel (NDC, circles), and Bonavista Corridor (BC, squares). The inset map outlines the study domain in eastern Canada. The relevant NAFO subdivisions 2J, 3K, and 3L boundaries are also indicated. Dashed lines represent 300 m depth contours. The bathymetry map is reproduced from GEBCO world map 2014 (www.gebco.net) and NAFO subdivisions reproduced from NAFO (www.nafo.int).

Table 2.1 Set details and diversity indices for 2013 Celtic Explorer data. Most abundant species (numbers, biomass) represents lists of the most frequently observed species pooled among sets within each region. Mean species richness and Simspon's reciprocal were generated based on all trawl sets with regions.

Region	Number of Sets	Most Abundant Species (Numbers)	Most Abundant Species (Biomass)	Mean Species Richness (± SD)	Mean Simpson's Reciprocal (± SD)
Hawke Channel	4	Redfish (26 – 88%)	Atlantic Cod (21 - 53%), Redfish (9 - 69%)	10.750 (± 2.754)	2.269 (± 0.992)
Notre Dame Channel	3	Atlantic Cod (4 - 65%), Redfish (24 - 83%)	Atlantic Cod (20 - 95%), Redfish (3 - 62%)	10.667 (± 2.081)	1.679 (± 0.352)
Bonavista Corridor	22	American Plaice (0 - 43%), Atlantic Cod (3 - 89%), Greenland Halibut (0 - 50%), Redfish (0 - 72%)	Atlantic Cod (1 - 99%), Greenland Halibut (0 - 60%), Redfish (0 - 96%)	13.212 (± 2.992)	3.588 (± 1.341)

Table 2.2 Set details and diversity indices for 2015 Celtic Explorer stomach data. Mean diet species richness and Simpson's reciprocal evenness data based on pooled fish samples within regions.

Region	Number of Sets	Number of Stomachs Analyzed	Mean Diet Species Richness (± SD)	Mean Diet Simpson's Reciprocal (± SD)
Hawke Channel	17	146	1.578 (± 0.846)	1.326 (± 0.515)
Notre Dame Channel	17	122	1.465 (± 0.731)	1.199 (± 0.384)
Bonavista Corridor	20	129	1.934 (± 1.149)	1.590 (± 0.835)

analysis resulted from multiple projects being conducted aboard the survey. Given the short period between the two surveys in addition to low frequency trends in community composition across this region during this time period (Pedersen et al. 2017), the community composition is unlikely to have shifted substantially between the two years.

Sample collection

All fish caught were sorted by species and their biomass was recorded. Sampled fish were swiftly killed with a sharp blow on the head. In 2015, fish selected for isotope analysis had their lengths measured for the following fish species, representing the most abundant species by sampled biomass (either over 5% of the caught fish species by biomass or by numbers): American plaice (*Hippoglossoides platessoides*, labelled 'Plaice' in figures), Atlantic cod (*Gadus morhua*, labelled 'Cod' in figures), capelin (*Mallotus villosus*), Greenland halibut (*Reinhardtius hippoglossoides*, labelled 'Turbot' in figures), lanternfish (N*otoscopelus* sp.), redfish (*Sebastes* sp.), and thorny skate (*Amblyraja radiata*, labelled 'Skate' in figures). We aimed to analyze twenty-one samples per species per region with as even a spread of sizes as possible. For species with little variation in size (capelin and lanternfish), only nine specimens were collected within each region. Based on the species' observed length distributions, sampled individuals were classified as small, medium, or large, by dividing the observed range of sizes into three length categories of equal width (Table 2.3; Table 2.S1). These categories are recognized to be arbitrary, but as the exact timing of potential ontogenetic shifts was unknown, this division accounted for variation across the range of observed sizes. From

Table 2.3 Definition of small, medium and large size categories for each species. Size category definitions were consistent across regions. See Fig 2.S1 for visual representation of species sizes.

Species	Small size range (cm)	Medium size range (cm)	Large size range (cm)
American Plaice	7.0 – 22.6	22.7 – 38.3	38.4 – 54.0
Atlantic Cod	13.0 – 45.9	46.0 – 80.0	80.1 – 113.0
Capelin	11.0 – 13.6	13.7 – 16.2	16.3 – 18.8
Greenland Halibut	10.0 – 27.4	27.5 – 45.0	45.1 – 62.5
Lanternfish	12.9 – 14.5	14.6 – 15.6	15.7 – 17.4
Redfish	4.0 – 18.6	18.7 – 33.2	33.3 – 48.0
Thorny Skate	10.2 – 33.9	34.0 – 58.3	58.4 – 80.0

most fish, a transverse sample of dorsal muscle tissue directly posterior to the head was collected, placed in 1.5 ml centrifuge vials and frozen at -20 ºC. Frozen stomach samples were also collected from these fish at sea. Stomachs from fish that showed signs of regurgitation or stomach eversion were not collected due to the potential of biasing stomach content results. The remaining fish with small, difficult to sample stomachs were individually labelled bagged, frozen whole at sea and later dissected in the laboratory for their muscle tissue and stomachs. Stomach content analyses identified and quantified the stomach contents to the lowest taxon feasible. Slow-dissolving features of prey, including otoliths, exoskeletons, and squid beaks were commonly used as prey identifiers. The mass and a count estimate of these prey were recorded with their identity.

Muscle tissue samples were oven dried at 75°C for 48 hours and homogenized using an amalgamator. The homogenized samples were weighed and analyzed at Cornell University Stable Isotope Laboratory (Ithaca, NY, USA). Approximately 1 mg of sample was placed into 7×7 mm tin capsules, then flash combusted using a Carlo-Erba NC2500

elemental analyzer coupled on-line to a Finnigan MAT Delta Plus mass spectrometer for analyses of the resulting carbon dioxide and nitrogen gases.

Species Richness and Diversity

Two indices were used to describe the three analyzed regions. Both indices were applied to each survey set separately and averaged within region. Species richness is a count of the number of fish species present within a given set. The Inverse Simpson index (Simpson 1945), defined as follows:

$$\lambda = 1/\sum_{i=1}^{S}(n_i/N)^2 \quad (1)$$

Where n_i is the total number of a given species *i* in a set, *N* is the total number of all species in a set, and S is the total number of fish species within a given set. This λ represents a probability that two randomly chosen individuals will be of different species, such that higher values represent higher diversities.

The analysis of species richness and diversity were undertaken using data from the May, 2013, ecosystem survey aboard the same vessel and covering the same areas as the 2015 survey (Fig 2.1). These data were used to characterize richness and diversity (both fish in the community and diet) due to superior data on species at the level of individuals beyond the large demersal species specifically targeted in 2015. Only fish species were analyzed for species richness and diversity while invertebrates were also included for diet diversity measurements within each fish stomach. While trawl data may provide representation for larger species and individuals, smaller fish may be underrepresented. Stomach content analysis has been proposed for assessing abundance of species that may not be

adequately represented in trawl data (Fahrig et al. 1993, Cook & Bundy 2012). Therefore, to assess the differences in potential prey available across regions, the contents of a total of 397 (303 of which contained prey) stomachs from all seven species analyzed in the 2015 survey were analyzed. Species richness and an ANOVA was used to test differences between regions with response variables of species richness or Inverse Simpson's Diversity and the categorical predictor variables of region and predator species.

Stable Isotope Calculation

Nitrogen and carbon ratios were expressed in delta (δ) notation, being the parts per thousand deviation from the standard material: Pee Dee belemnite limestone for carbon and atmospheric nitrogen for nitrogen as follows:

$$\delta^{15}N \text{ or } \delta^{13}C = \left(\left(\frac{-R_{sample}-}{R_{standard}}\right) - 1\right) \times 1000 \quad (2)$$

$$R = {}^{13}C/{}^{12}C \text{ or } {}^{15}N/{}^{14}N \quad (3)$$

Lipids were not removed to avoid the potential influence of derived products on isotopic signatures (Pinnegar & Polunin 1999). Therefore, following analysis, the δ^{13}C values were normalized for lipid bias as recommended by (Post et al. 2007), as follows:

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C{:}N \quad (4)$$

As the majority of fish samples were close to a C:N ratio of 3.3 as would be expected for muscle tissue of marine fish (Ricklefs & Travis 1980), this adjustment was only particularly relevant for lipid rich fish such as capelin, lanternfish and Greenland halibut.

Regional and ontogenetic variation was assessed using an ANCOVA on the following GLM:

$$\delta^{15}N \; or \; \delta^{13}C \; = \text{Region} * \text{Length} \quad (5)$$

With region being a categorical variable (n = 3) and length as a continuous variable. This analysis was conducted for each species separately.

Bayesian Ellipses

The remaining isotope analyses were conducted in two ways: (a) using size-pooled data as has frequently been done in such analyses and (b) splitting each species into three size categories to assess the influence of ontogenetic variation on metrics of niche overlap. The first of the Layman metrics was the Bayesian ellipse overlap, representing the core isotopic niche space occupied by a species. The construction of Bayesian ellipses, corrected for low sample size, was conducted in the R package SIBER (Jackson et al. 2011). Analyses were conducted among species, not among size groups within species. The standard Bayesian ellipses represent the core isotopic niche space and represent bivariate standard deviation. The overlap between ellipses in isotopic space reflects overlap in the isotopic niches (Jackson et al. 2011). The proportion of overlapping ellipses is a count of the number of instances in which two Bayesian ellipses overlap in isotope biplot space over the total number of potential overlaps. The percent overlap is given by the percent of the overlapping area over the total area covered by the two ellipses. A mean of these overlapping areas was calculated for each region. An increased overlapping area represents increased isotopic niche overlap between the two species.

Mean Distance to Centroid and Nearest Neighbour

For the purposes of this study, the community centroid was considered as the mean carbon and nitrogen values of the centers of each species' ellipse (sizes pooled). The distance to the centroid is therefore defined as the distance between the centers of each ellipse to the community centroid within each region (Layman et al. 2007). This provides an indication of the degree of trophic diversity within a food web such that high mean distances indicate a wide variety of isotopic niches and low distances indicate a limited diversity of niches. The mean of these distances to the centroid was then calculated for each region. The distance to the nearest neighbour is calculated by analyzing the distance in biplot space between the center of a given ellipse and the center of each other ellipse of different species and selecting the shortest distance (Ricklefs & Travis 1980). The mean of the distance represents the overall density of species packing in trophic niche space such that high values indicate wider spread within biplot space while lower values indicate higher density of niches and trophic redundancy. The standard deviation of the distance provide a measure of evenness of species packing in biplot space such that high values indicate skewed spreads of isotopic niches and low values indicate even spread of niches. The mean and standard deviation of the shortest distance to the neighbouring ellipses was then calculated for these measured shortest distances. A general linear model was constructed with response variables of either mean distance to the centroid or the mean nearest neighbour and the categorical predictor variable of region (n=3). Bootstrapping was conducted on the mean and standard deviation distance to nearest neighbour to determine the credible interval around the calculated metrics.

Results

Species Richness and Diversity

No differences in the mean tow duration were observed among the three regions analyzed in the 2013 survey, allowing for comparison of the three regions ($p = 0.28$ from a one-way ANOVA). The Inverse Simpson's Index based on fishes sampled, was found to vary significantly among regions ($p = 0.05$) with Bonavista Corridor being the most diverse and the Notre Dame Channel the least diverse (Table 2.1). The sets in the northern two regions were dominated by one or two fish species (Atlantic cod and redfish) based on percentage of total catch while sets in the Bonavista Corridor were characterized by a more even representation of fish abundances among species (Table 2.1). In contrast, mean fish species richness within survey sets did not differ significantly among the three regions ($p = 0.25$) (Table 2.1).

The Simpson's Inverse diversity of the stomach contents was higher in the Bonavista Corridor than the other two regions ($p < 0.01$; Table 2.2), as was previously observed in these regions (Krumsick & Rose, 2012). Similarly, prey species richness was significantly higher in the Bonavista Corridor than the two northern regions ($p < 0.01$). These trends were consistent across all species except the nearly-exclusively planktivorous lanternfish and capelin. A summary of these stomach content analyses are included in Fig. 2.S2 and 2.S3.

Stable Isotopes

Significant ontogenetic change in nitrogen signatures were observed in five of seven fishes examined (Figs 2.2-2.3). Nitrogen signatures increased with length for American plaice ($p < 0.01$), Atlantic cod ($p < 0.01$), Greenland halibut ($p < 0.01$), lanternfish ($p < 0.01$) and redfish ($p < 0.01$). As these species increased in size the nitrogen isotopic value increased indicating that larger individuals were feeding at a higher trophic level. Among regions, Atlantic cod ($p < 0.01$) and Greenland halibut ($p < 0.01$) were found to show significantly lower nitrogen signatures in the northern regions while American plaice ($p = 0.01$) and redfish ($p < 0.01$) exhibited higher values in the north (Fig 2.2). Capelin and

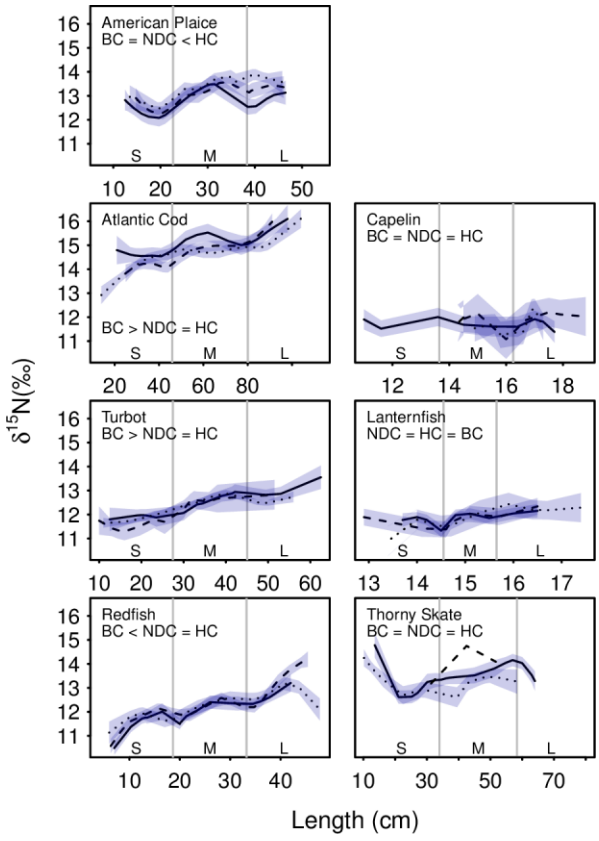
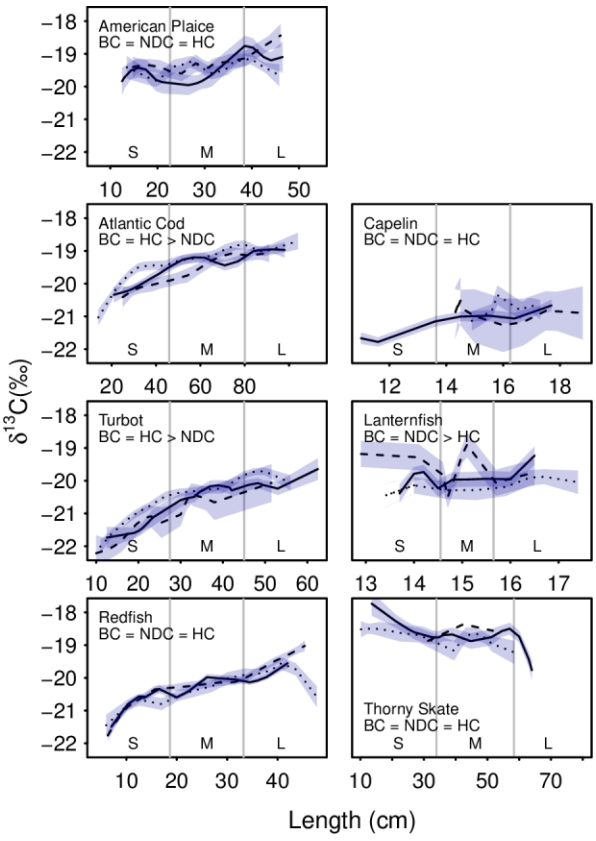


Fig. 2.2 Nitrogen isotopic values across the seven species and three size classes (small, medium, large). Lines were fitted using local polynomial regression ($\alpha = 0.5$) and the line type indicates region (solid: Bonavista Corridor; dashed: Notre Dame Channel; dotted: Hawke Channel). Error bars represent the standard error (except for Notre Dame thorny skate due to low sample size). For definitions of size categories, refer to Table 2.3.



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thorny skate nitrogen signatures did not vary with length or region.

Carbon isotopic values generally increased with size for six of the seven species analyzed (Fig 2.3). With increasing size American plaice ($p < 0.01$), Atlantic cod ($p < 0.01$), Greenland halibut ($p < 0.01$), and redfish ($p < 0.01$) shifted from a zooplankton-dominated diet to a mixed pelagic/benthic based diet, while thorny skate ($p < 0.01$) shifted from a benthos-dominated diet towards a mixed pelagic/benthic diet. Atlantic cod ($p = 0.02$), Greenland halibut ($p = 0.01$) and lanternfish ($p = 0.03$) showed regional variation with their carbon signatures. Capelin carbon isotopic values did not vary with length or region.

Bayesian Ellipses

The proportions of overlapping Bayesian ellipses tended to increase with decreasing species diversity as did the percent overlap of these ellipses (Figs 2.4-2.7, Table 2.4). The Bonavista Corridor had the greatest spread of core isotopic niches in biplot space. However, in other regions, where prey diversity decreased, these core isotopic niches overlapped more and trended towards the center of the biplot, suggesting increased competition for less diverse prey resources (Table 2.4). Finally, the pooled and size-category separated analyses illustrated that while pooling all sizes within species together provided a general idea of the isotopic niche a species filled within the community, pooling increases perceived overlap in all cases (Table 2.4).

Mean Distance to Centroid

Region appeared to be important to explaining the distance of some species/size combination from the community centroid (Table 2.5), particularly Atlantic cod ($p = 0.01$) and capelin ($p = 0.03$). Species in the Hawke Channel were closer to the community centroid in almost all cases compared to those in the Bonavista Corridor. The Notre Dame Channel samples often exhibited erratic behavior that did not consistently follow trends of diversity, though overall the community tended to be closer to the centroid in regions with lower prey diversity. As species increased in size, capelin ($p = 0.04$), Greenland halibut ($p < 0.01$), lanternfish ($p = 0.03$), and redfish ($p < 0.01$) tended to gravitate towards the community centroid. Atlantic cod ($p < 0.01$) were found to stray away from the centroid with increased size.

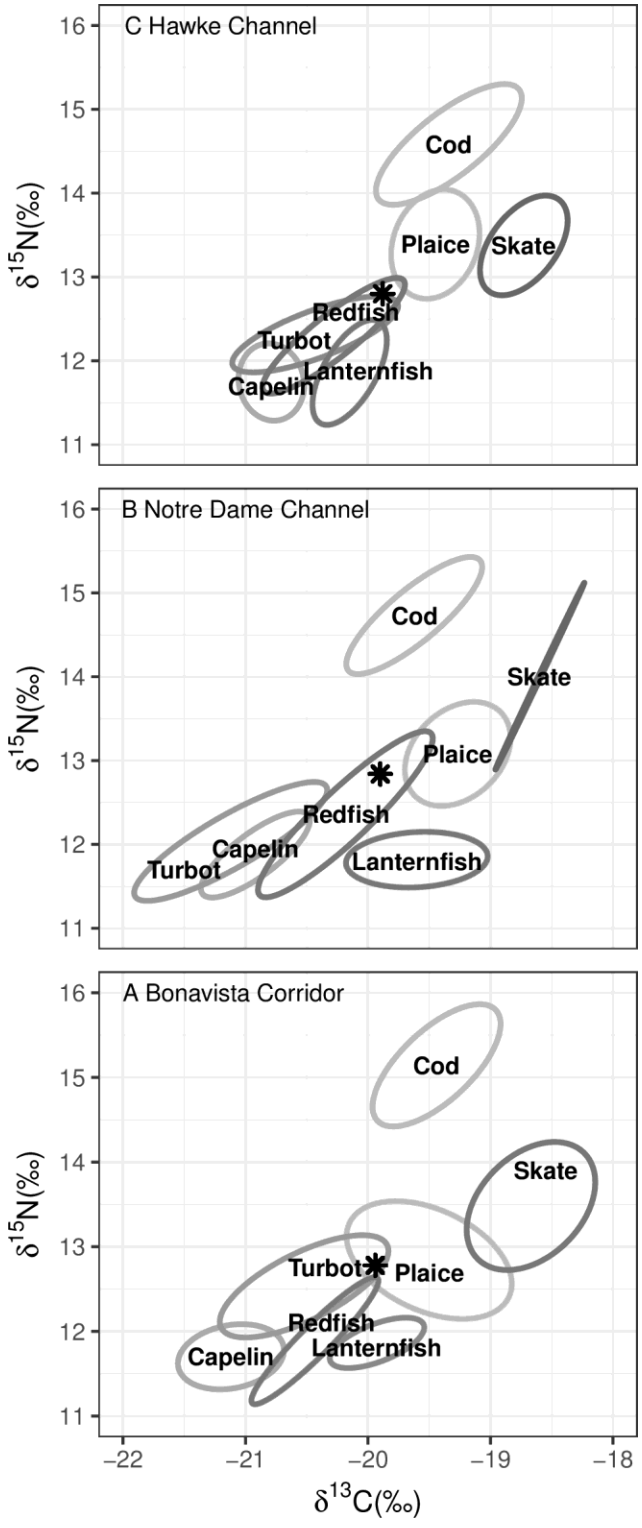

Fig. 2.4 Representation of Bayesian ellipses within stable isotope biplot space for the seven species with all size classes combined. The δ^{15}N axis represents the relative trophic level with lower trophic levels towards the bottom and higher trophic levels towards the top. The δ^{13}C axis represents the relative contributions of the base of the food web to the upper food web with pelagic contributions to the left and benthic/detrital contributions to the right. Individual panels represent: (a) Bonavista Corridor, (b) Notre Dame Channel, and (c) Hawke Channel. The star represents the community centroid within each region.

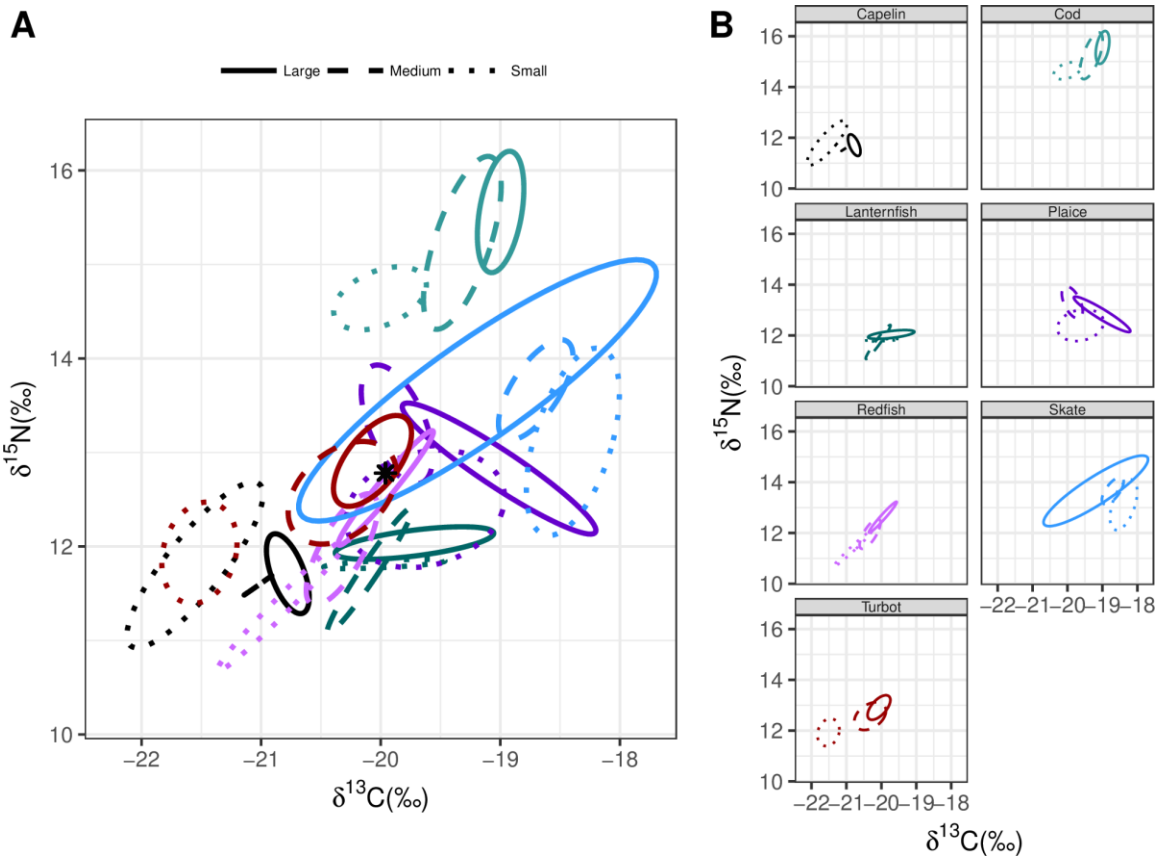

Fig. 2.5 Representation of Bayesian ellipses within stable isotope biplot space for the seven species within the Bonavista Corridor separated by size class. The δ^{15}N axis represents the relative trophic level with lower trophic levels towards the bottom and higher trophic levels towards the top. The δ^{13}C axis represents the relative contributions of the base of the food web to the upper food web with pelagic contributions to the left and benthic/detrital contributions to the right

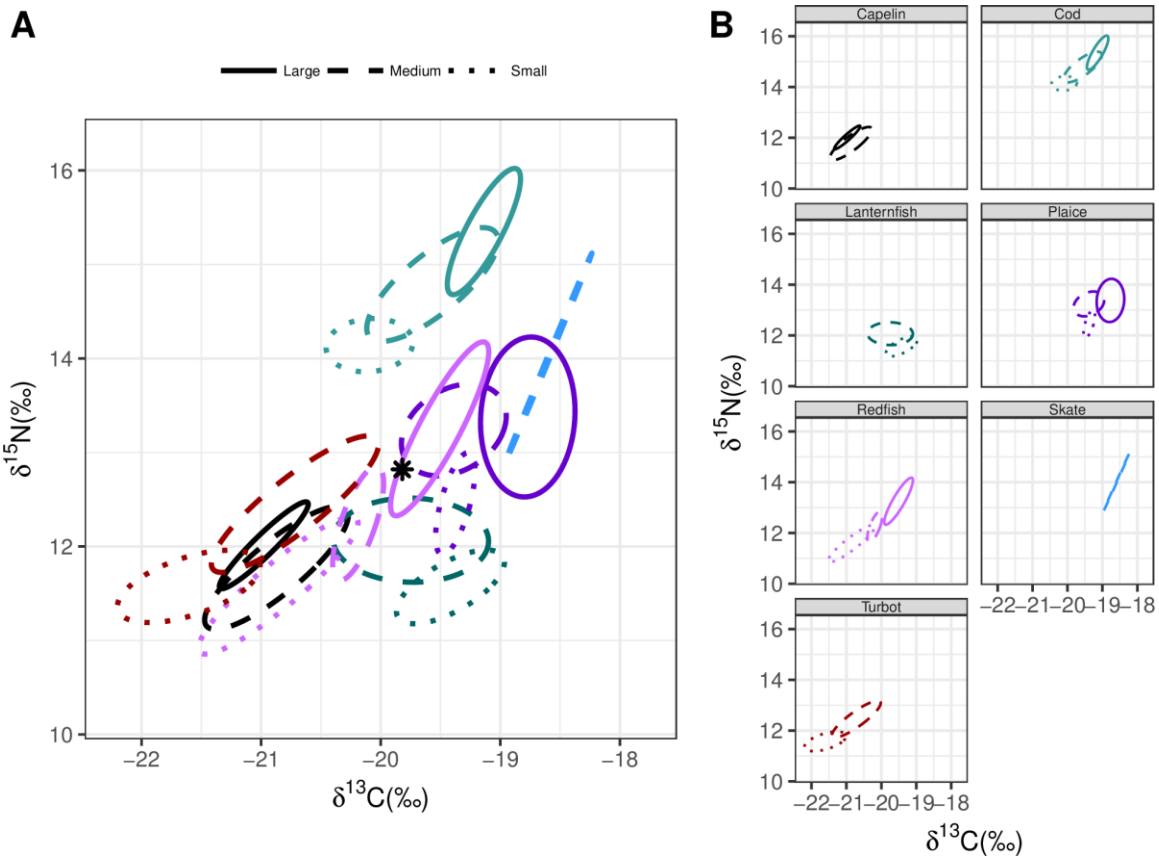

Fig. 2.6 Representation of Bayesian ellipses within stable isotope biplot space for the seven species within the Notre Dame Channel separated by size class. The δ^{15}N axis represents the relative trophic level with lower trophic levels towards the bottom and higher trophic levels towards the top. The δ^{13}C axis represents the relative contributions of the base of the food web to the upper food web with pelagic contributions to the left and benthic/detrital contributions to the right

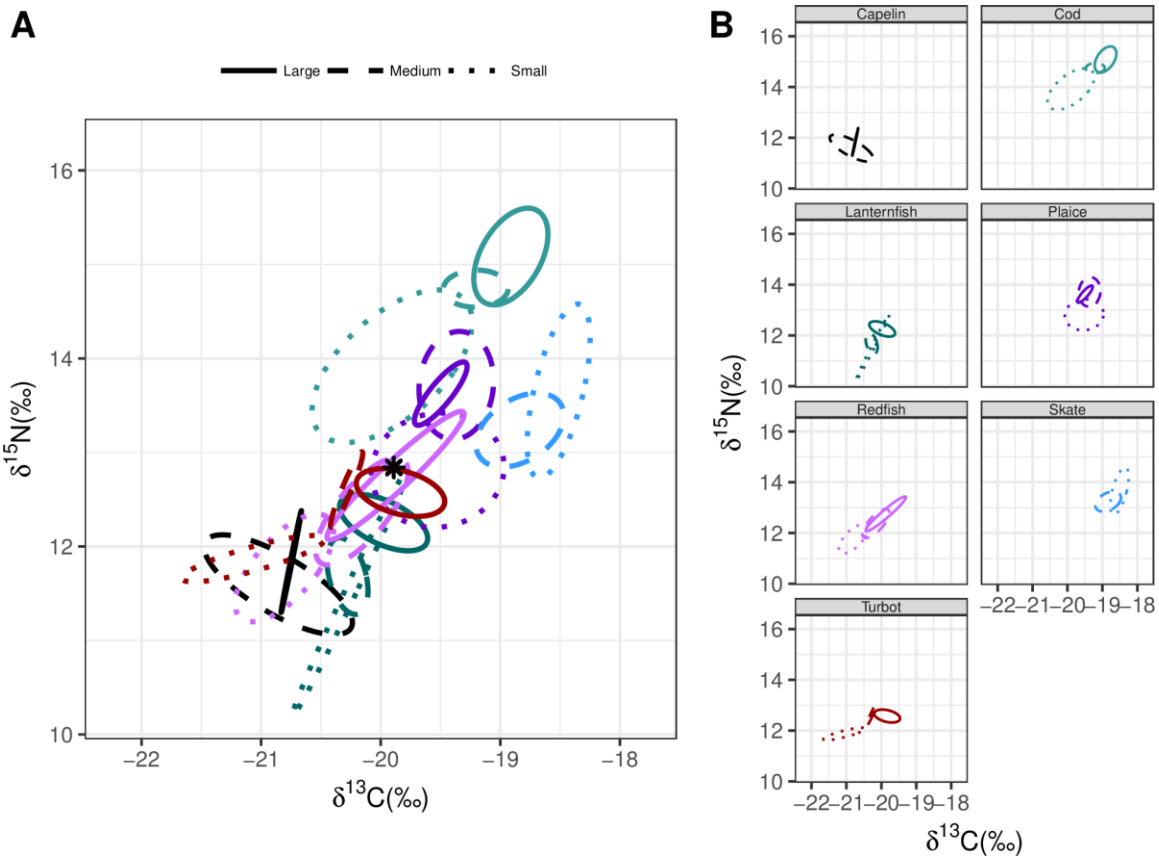

Fig. 2.7 Representation of Bayesian ellipses within stable isotope biplot space for the seven species within the Hawke Channel separated by size class. The δ^{15}N axis represents the relative trophic level with lower trophic levels towards the bottom and higher trophic levels towards the top. The δ^{13}C axis represents the relative contributions of the base of the food web to the upper food web with pelagic contributions to the left and benthic/detrital contributions to the right

Table 2.4 The proportion of observed overlapped Bayesian ellipses, mean % overlap area of ellipses (± SE) and mean and standard deviation for distance to nearest neighbour (DNN; ± bootstrap CI). Includes analysis for the exclusion (Fig 2.4) and inclusion of size categories (Figs 2.5-2.7).

Region	Sizes Separated				Sizes Pooled			
	Proportion of overlaps	Mean % overlap	Mean DNN	Standard Deviation DNN	Proportion of overlaps	Mean % overlap	Mean DNN	Standard Deviation DNN
Hawke Channel	0.23	2.07 (± 0.47)	0.46 (± 0.02)	0.37 (± 0.04)	0.36	4.01 (± 2.22)	0.58 (± 0.12)	0.37 (± 0.16)
Notre Dame Channel	0.19	1.88 (± 0.55)	0.58 (± 0.04)	0.39 (± 0.20)	0.24	1.47 (± 1.00)	0.81 (± 0.16)	0.42 (± 0.16)
Bonavista Corridor	0.16	1.52 (± 0.38)	0.58 (± 0.04)	0.47 (± 0.06)	0.27	0.84 (± 0.36)	0.90 (± 0.16)	0.47 (± 0.14)

Table 2.5 Mean distance to the centroid (± SE) by region for size-pooled (Fig 2.4) and size-divided ellipses (Figs 2.5-2.7). HC standing for Hawke Channel, NDC for Notre Dame Channel, and BC for Bonavista Corridor.

Region	Small	Medium	Large	Pooled
HC	1.22 (± 0.40)	1.14 (± 0.43)	1.06 (± 0.46)	1.09 (± 0.17)
NDC	1.42 (± 0.53)	1.20 (± 0.45)	1.31 (± 0.49)	1.26 (± 0.19)
BC	1.46 (± 0.20)	1.22 (± 0.28)	1.07 (± 0.41)	1.21 (± 0.25)

Mean Distance and Standard Deviation to Nearest Neighbour

The Hawke Channel fish species showed the closest proximity to their nearest neighbour and had the lowest standard deviation, indicating that individuals were more tightly packed within the isotope space, associated with increased trophic redundancy and/or competition (Table 2.4). The Bonavista Corridor showed a higher distance to the nearest neighbor and highest standard deviation, indicating the widest spread in niche space. In

comparison to these regions, the Notre Dame Channel had the highest mean distance to nearest neighbour. The mean distances to the nearest neighbour generally decreased when considering within species sizes separated rather than pooled (similar to Bayesian overlap; Table 2.4). This similarity indicates that not incorporating size variation within species tends to inflate average distances among species (Table 2.4).

Discussion

To understand interactions within recovering fish communities in Newfoundland and Labrador, I investigated how regional variation in fish and prey diversity, and fish size, influence four stable isotope metrics of community trophic structure. Trends in fish and prey diversity followed trends in the four metrics, indicating the potential importance of diversity in determining a species' isotopic niche. Our study further quantified the importance of considering ontogenetic shifts in Bayesian ellipse analyses of community trophic structure.

Ontogenetic shifts in diet were found in nearly all species studied. Species that exhibited increased trophic levels with size, such as Atlantic cod and redfish, were found to incorporate more fish into otherwise invertebrate-dominated diets (Fig 2.S2). Pelagic feeders, such as redfish and Greenland halibut, incorporated more benthically derived prey into their diets with increasing size, frequently switching from diets dominated by zooplankton to incorporate more shrimp and small fish. Similarly, benthic feeders, such as thorny skate, showed more pelagically derived prey as demonstrated by decreases in carbon signature, shifting from a benthic invertebrate dominated diet to incorporate more

zooplankton. These observations are often consistent with trends observed in the stomach contents of these fish species (Fig 2.S2). Capelin, which did not vary with size in their carbon or nitrogen isotopes, demonstrated no change in their diet associated with size, consuming nearly entirely zooplankton at all observed sizes.

Numerous studies report ontogenetic shifts within a given species (e.g. Quevedo et al. 2009, Matley et al. 2013, Albo-Puigserver et al. 2015), yet few assess the importance of ontogenetic shifts on community structure (e.g. Zhao et al. 2014). The vast majority of previous analyses that utilize stable isotopes and Bayesian ellipses group individuals together without intraspecific size considerations. If a species exhibits altered isotopic niches with ontogeny they would experience variable niche overlaps with different species (Nakazawa 2015). While pooling the size categories by species may provide a general idea of the trophic role filled by the organism, such an approach will overlook complexities in ontogenetic niche shifts and niche overlap across the life stages of the species. This pooling also leads to higher estimates of both proportions of niche overlap and mean percentage niche overlap vs. analyses that consider categories of fish size categories (Table 2.4).

An additional result of this study is that, with the exception of Atlantic cod, with increased size a species' core isotopic niches trended towards a community centroid. With increasing body size gape size increases, expanding the range of feeding opportunities (Werner & Gilliam 1984, Woodward & Hildrew 2002). Increased size additionally allows for more efficient predation and generalized feeding, as much as the local food web allows, resulting in a trend towards to the centroid. These trends are also

frequently associated with increases in the nitrogen signature, indicating an increased trophic level at which the predators feed with increased size. Atlantic cod, however, represents the top opportunistic fish predator sampled within this ecosystem and as such fills its own unique ecological niche (Popova 1962, Link et al. 2009). It is important to note that both the 2013 and 2015 ecosystem surveys often targeted aggregations of dominant cod and/or redfish (Rose & Rowe 2015). The diversity indices therefore may reflect the ecosystem as less diverse than what would expect from random sampling. This sampling pattern, however, was consistent across all sets. The variation observed in the diversity indices among regions therefore likely reflect underlying ecosystem variation.

Regional variation and related fish/prey diversity were related to isotopic niches in biplot space. The northern regions of this study (Hawke and Notre Dame Channels) exhibited reduced richness and evenness in both predator occurrences and predator diets. As such we would anticipate that species would be less capable of avoiding niche overlap as observed in the present study with an increased number and percent of overlap ellipse areas in northern regions. This would explain why the distance to the community centroid and mean/standard deviation of the distance to the nearest neighbor decreased between the Bonavista Corridor and the Hawke Channel and the degree of overlap of the Bayesian ellipses increased. The only species that were found to increase their trophic level in the northern regions was American Plaice, which was found to consume more demersal fish and crab in place of shrimp, and redfish, which was found to consume more shrimp and crab and less zooplankton. Species that demonstrated a decrease in trophic level, such as turbot, were found to consume fewer fish and more invertebrate prey (Fig 2.S3).

Of particular interest to the Newfoundland and Labrador area are the variable observed recovery rates of Atlantic cod across regions. The Bonavista Corridor exhibited notable recovery rates, while the northern regions have experienced slower recovery rates as well as reduced growth and condition from their depletion during the late 1980's and early 1990's (Lilly et al. 2008, Rose & Rowe 2015, Morgan et al 2018, DFO 2018). The cod in the Notre Dame and Hawke Channels have been shown to frequently intermix and are genetically indistinguishable, yet the southern fish populations show minimal overlap with the northern populations and are genetically distinguishable (Bentzen et al. 1996, Taggart 1997). Thus while the northern cod is managed as a stock complex (DFO 2018), it contains a number of partially isolated subcomponents (Templeman 1979, Smedbol & Wroblewski 2002). Recovery of these subpopulations could therefore come from two potential sources: recolonization from other subpopulations or resurgence of the local subpopulation (Smedbol & Wroblewski 2002, Rose & Rowe 2018). In either case (or some combination of the two mechanisms), the subpopulations exhibit variability in the isotopic niche and presumably trophic niches.

Numerous other biological explanations have been provided for the variable recovery rates among these populations, including decreases in prey availability (particularly capelin) and increased predation (Rose & O'Driscoll 2002, Sherwood et al. 2007, Buren et al. 2014, Mullowney & Rose 2014, Skern-Mauritzen et al. 2016). Our results suggest another potential component: spatial variation in trophic overlap as evidence of higher potential competitive interactions in northern regions. In the Bonavista Corridor, Atlantic cod occupies a unique niche space at the upper part of the food web with no overlap in

their core isotopic niche with any of the analyzed species (Figs 2.4-2.7). While still a top predator in the Notre Dame and Hawke Channels, Atlantic cod trophic level decreases. In the Hawke Channel in particular more ellipse overlap with other species is observed, particularly between juvenile cod and other species. In the Hawke and Notre Dame Channels, prior analyses from the years 1997 to 2011, consistent with the results of this study, have revealed that the diet of cod is heavily dominated by shrimp (55 - 99 % of diet by weight) while fish species in the Bonavista Corridor make up a more substantial portion of the stomach contents (15 - 71% by weight) with overall higher fullness indices (Sherwood et al. 2007, Krumsick & Rose 2012). In all regions, as the cod increased in size they deviated away from the centroid and thereby reduced trophic overlap and potential competition with other species. It should be noted that competition could not be concluded as this would require knowledge of the relative abundance of prey items, which I did not have data to assess, but the results nonetheless have implications for the possibility of competition. The sizes that are most affected by this overlap would be primarily the small cod, which would include the juveniles and young adults. This feeding at a lower trophic level in small quantities relative to body mass (Krumsick & Rose 2012) with increased isotopic niche overlap with other species together would represent an ontogenetic bottleneck which could limit the success of cod populations in the northern regions. Although competitive interactions are likely not the sole explanation for observed variability in recovery rates, it seems a potential factor.

Our results also illustrate how Atlantic cod fill a unique role within the fish community. While overlaps do occur with other species at smaller sizes in areas with

reduced prey diversity, these fish appear to occupy a unique ecological niche. The other analyzed species typically exhibited much more substantial overlap in their Bayesian ellipses and presumably also in competition pressures. This unique position occupied by cod within the food web as a dominant fish predator could account for the cod's success and abundance within this ecosystem prior to human exploitation.

There are survey spatial design issues that require consideration. For example, there is little spatial overlapv between the 2013 and 2015 survey in the Hawke and the Notre Dame Channels. However, given the consistent trends in diversity of the catch trends with the stomach data (Tables 2.1-2.2), the issue of spatial overlap is unlikely to have a significant impact on our results. In both years, the number of sets deployed in the Bonavista Corridor exceeded those in either the Hawke Channel or the Notre Dame Channel. Due to this limited number of sets, many of the isotope sample sizes were smaller, particularly in these northern regions. As the sampling was entirely opportunistic, sufficient sample sizes for certain size classes of some species (such as capelin) were simply not available. In cases where sample sizes were lower, two competing processes could influence our results, as demonstrated clearly with the case example of thorny skate. One could anticipate an increase in the size of the standard ellipses as the mathematical result of reducing sample size, as appears to be the case with large thorny skate in the Bonavista Corridor such that it occupies a large plot area (Fig 2.5). However, with decreased sample sizes could also underrepresent potential diet variability resulting in smaller ellipse areas, as is likely the case with thorny skate in the Notre Dame Channel where the ellipse appears almost as a straight line (Fig 2.6).

Consideration of these errors presented here as examples serve to further support our hypotheses, as thorny skate overlap in the Bonavista Corridor would be overestimated and underestimated in the Notre Dame Channel.

Historically worldwide there has been little ecosystem focus in fisheries assessment and management decisions (Slocombe 1993). Single-species approaches have often failed and the state of many ocean ecosystems continued to decline (Slocombe 1993, Pikitch et al. 2004). Ecosystems, however, are complex adaptive systems such that understanding of the interconnection of components is essential in order to assess how species interactions and population dynamics will change (Levin 1998). Therefore investigating the interactions of various components of an ecosystem is essential for ecosystem approaches within fisheries assessment and management (Fowler 1999, Rice 2000). Understanding multispecies trophic niche structure and how isotopic niches are associated with ontogenetic shifts may help reveal a species' ecological role and what competitive pressures it may experience.

Knowledge of the present state of the ecosystem allows for the establishment of a baseline by which we can assess future potential environmental changes on isotopic niches. In the recovering and dynamic ecosystem we are presently observing in Newfoundland and Labrador, prey identities and quality are changing (Davoren & Montevecchi 2003, Dwyer et al. 2010, Dawe et al. 2012). These studies predict an overall decreased prey field such that increased competition is likely to occur for a lower diversity of lower quality prey species. Should trends continue in this fashion, we would anticipate the regions occupied by Bayesian ellipses would trend towards increased

interspecies overlap, as was observed in northern regions where recovery has not been observed (Rose & Rowe 2015, DFO 2018). However, should ecosystem recovery occur approaching an unexploited ecosystem state with increased prey diversity, we might anticipate this trend to be reversed such that core isotopic niches within biplot space exhibit greater spread and decreased overlap with the isotopic niches of other species.

The regional differences characterized in this study follow trends observed in other marine ecosystems. The observed decrease in species packing with decreasing latitude as well as an increased overlap in Bayesian ellipses have been observed in other temperate to polar environments (Saporiti et al. 2015, Linnebjerg et al. 2016). Furthermore, tropical and sub-tropical study regions frequently showed lower degrees of trophic overlap (e.g. Heithaus et al. 2013, Tilley et al. 2013, Albo-Puigserver et al. 2015), though there are exceptions (Brosset et al. 2016, Frisch et al. 2016). These studies did not connect any observed geographic variation to species richness or diversity but rather to factors such as latitude or salinity gradients (e.g. Saporiti et al. 2015, Brosset et al. 2016).

I have shown that niche overlap and potential competitive interactions, as revealed by each species respective position in isotope biplot space, are associated with the biodiversity of available prey. With fewer options available, more overlap in biplot space was observed. With greater prey diversity species spread to fill the available isotopic/trophic niches. However, these trends are also counteracted by the fact that in warmer waters in addition to more available prey species there will also be more predatory species that could potentially be competition. To further understand and establish a baseline for the present trophic structure of this marine ecosystem we require a

more detailed understanding of predator-prey interactions that underlie these results, providing inspiration for future work presently underway.

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Supplementary Information

Table 2.S1: Isotope sample sizes by region and size category with stomach sample sizes containing prey in parentheses.

	Region	Small	Medium	Large
American Plaice	HC	4 (4)	10 (20)	7 (2)
	NDC	5 (0)	12 (2)	4 (0)
	BC	7 (4)	7 (7)	7 (2)
Atlantic Cod	HC	7 (3)	8 (3)	6 (2)
	NDC	7 (4)	9 (8)	4 (3)
	BC	7 (6)	7 (7)	7 (3)
Capelin	HC	0	3 (2)	5 (4)
	NDC	0	5 (14)	4 (17)
	BC	3 (3)	3 (6)	3 (5)
Greenland Halibut	HC	8 (10)	7 (7)	6 (2)
	NDC	8 (13)	7 (2)	1
	BC	5 (3)	9 (3)	7 (9)
Lanternfish	HC	3 (7)	3 (15)	4 (8)
	NDC	3 (3)	4 (3)	2 (2)
	BC	3 (5)	3 (4)	3 (3)
Redfish	HC	5 (1)	8 (13)	8 (2)
	NDC	7 (9)	7 (2)	7 (3)
	BC	7 (3)	7 (3)	7 (1)
Thorny Skate	HC	8 (5)	9 (6)	1 (1)
	NDC	0	3 (0)	0
	BC	7 (9)	11 (14)	3 (3)

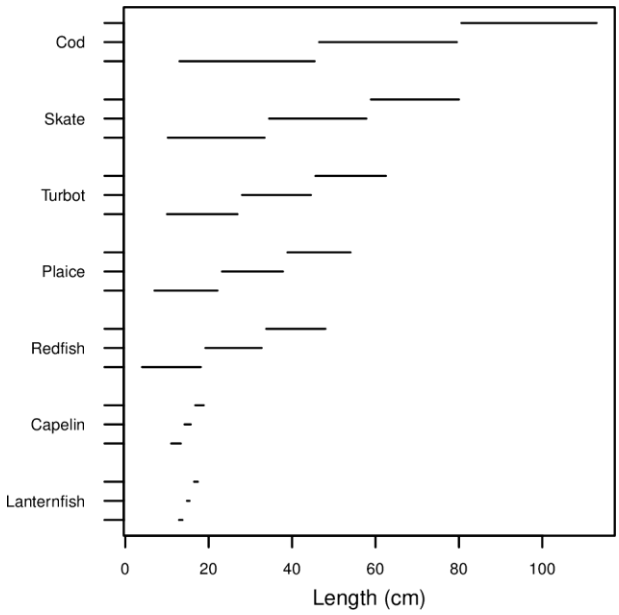


Fig. 2.S1 Visual representation of size class definitions (small, medium, large) within and among species analyzed.

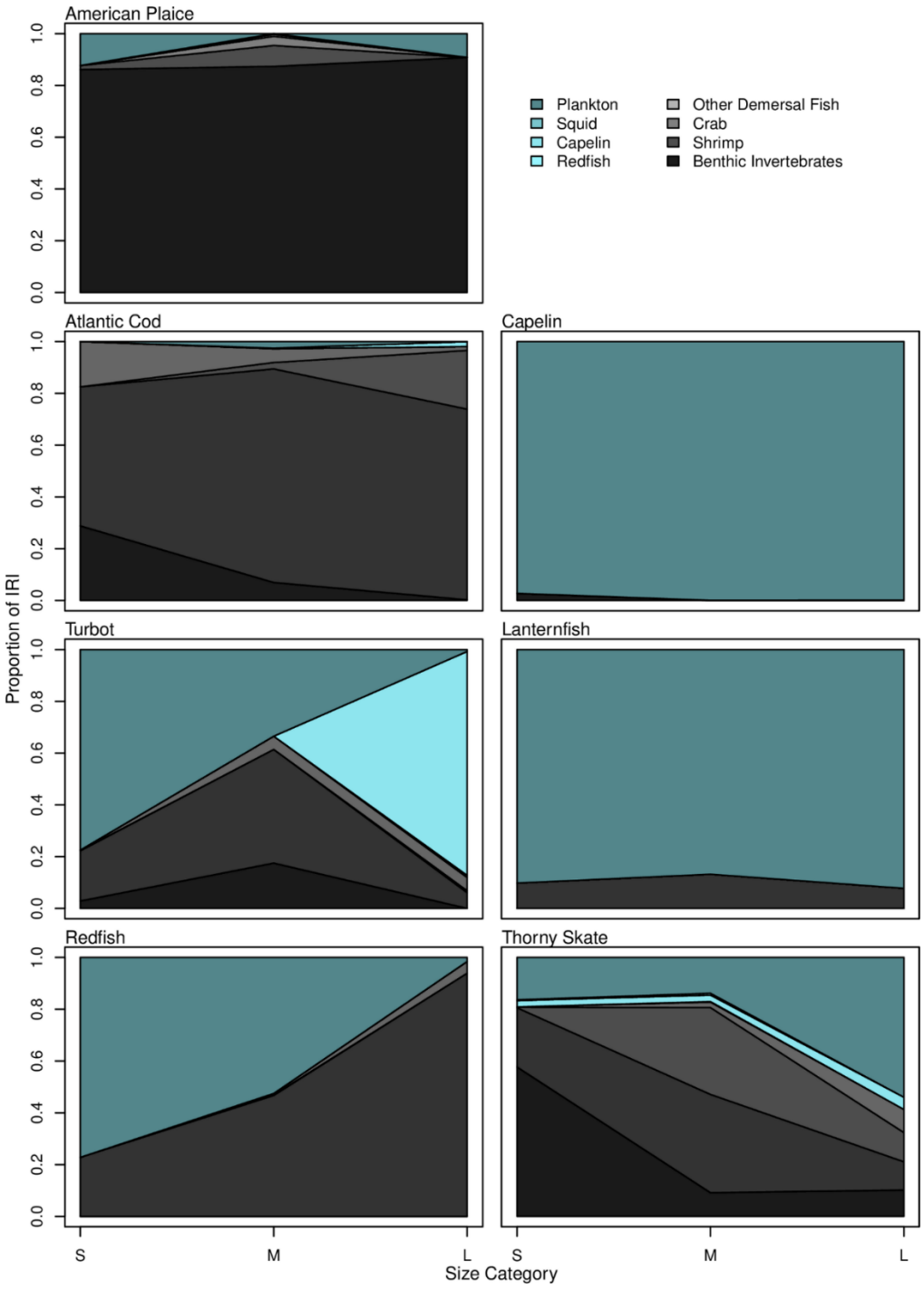


Fig. 2.S2 Proportion represented by the Index of Relative Importance (IRI) of eight major prey groups by size category. Individual stomach contents were pooled by species and size category. The IRI is defined as IRI = (%N + %B)/FO, where %N is the percent by number, the %B the percent by biomass, and FO the frequency of occurrence (Stevens et al. 1982). Blue colours represent pelagic prey while grey colours represent benthic prey.

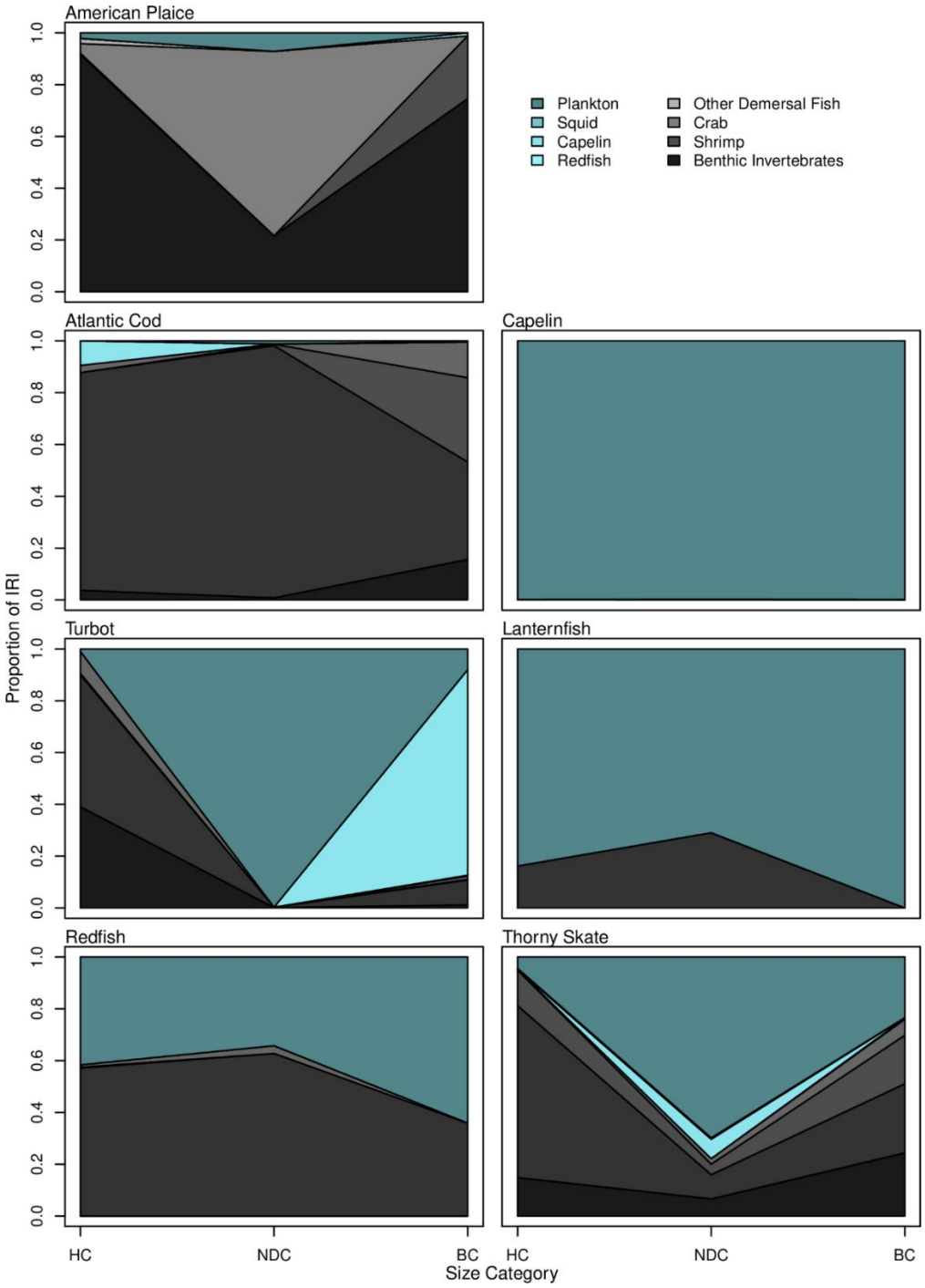


Fig. 2.S3 Proportion represented by the Index of Relative Importance (IRI) of eight major prey groups by region. Individual stomach contents were pooled by species and region**.** The IRI is defined as IRI = (%N + %B)/FO, where %N is the percent by number, the %B the percent by biomass, and FO the frequency of occurrence (Stevens et al. 1982). Blue colours represent pelagic prey while grey colours represent benthic prey.

Chapter 3: Regional Spatial Variation in Food Web Structure and Functioning Among Newfoundland and Labrador Fish Assemblages.

Abstract

Recently spatial heterogeneity associated with ecosystem diversity was reported from isotopic niche analysis for the offshore Newfoundland and Labrador shelf ecosystem. In order to assess the underlying processes driving these trends, we quantified species interactions using stable isotope mixing models. Representative samples of each species caught in trawls and plankton tows were collected for stomach content and stable isotope ($\delta^{15}N$ and $\delta^{13}C$) analyses to parameterize isotope mixing models. Regional variation, highlighted by the diets of three economically important species, was observed such that the southern region showed higher consumption of fishes, brittlestars and copepods while higher consumption of shrimp characterized northern regions. Food web metrics indicated that the low-diversity northern regions had higher connectance and shorter food chain length. The benthic portion of the community increased relative to the size of the pelagic portions in these northern regions. Regional variation in prey consumption contributes to differential competition among predators and associated differences in fish community recovery.

Introduction

The collapse of demersal fish stocks off Newfoundland and Labrador brought about ecosystem changes by reducing the influence of dominant top predators (Lilly et al.

2000). One impact of this change was influencing interactions among species through predation and indirect effects (Windle et al. 2012). Now, more than two decades after stock collapses and associated fisheries moratoria the ecosystem has still not fully recovered (Pedersen et al. 2017, Chapter 4). Factors influencing this trajectory include continued fishing (Shelton et al. 2006), depensation (Shelton and Healey 1999), climate change (Sguotti et al. 2019), and life history changes (Olsen et al. 2004). However, Newfoundland and Labrador marine ecosystems also exhibit spatial heterogeneity in their structure and function with northern communities displaying lower fish species diversity (Krumsick & Rose 2012, Chapter 2), and lower recovery of marine fish community size-structure (Chapter 4). Considering these findings, it is important to quantify the extent to which spatial variability in diets on relevant timescales is related to these patterns.

Given interest in the application of ecosystem-based analyses to fisheries management, understanding food-web interactions and their contribution to species and community dynamics has become essential (Pikitch et al. 2004, Crowder et al. 2008, Fulton et al. 2014). Quantifying trophic interactions has relied on various methodologies and tools including stomach content analysis (Hynes 1950, Hyslop 1980), fatty acid analyses (Kharlamenko et al. 1995, Kiyashko et al. 1998, Parrish et al. 2000), pyrosequencing of prey DNA from stomach contents or faeces (Symondson 2002, King et al. 2008, Deagle et al. 2009), and stable isotope analyses (Post 2002).

Stable isotope analysis constitutes the primary technique that has been used to supplement traditional stomach content analysis for assessing energy flow through an ecosystem over longer periods (Fry 2006, Lorrain *et al.* 2002). Studies of stable isotopes

in ecology provide information on the origins and consequent assimilation of organic matter which provide insight into the food web as a whole (Peterson *et al.* 1985, Owens 1987, Peterson & Fry 1987, Bunn & Boon 1993). The stable nitrogen isotope signature ($\delta^{15}N$) typically becomes enriched by approximately 3 ‰ for fish species with each consumption due to preferential removal of lighter amine groups during deamination, allowing for approximation of trophic level (Macko *et al.* 1982, Minagawa & Wada 1984, Vander Zanden *et al.* 1997). The stable carbon isotope signature ($\delta^{13}C$) provides an indication of the initial carbon source (pelagic or benthic/detrital in origin) and enriches at typically less than 1 ‰ with fractionation frequently considered negligible (DeNiro and Epstein 1978, Hecky & Hesslein 1995, Vander Zanden et al. 2001). Together these two isotope values can be used to determine isotopic niches which are thought to be proxies of trophic niches (Bearhop et al. 2004, Newsome et al. 2007, Chapter 2). With additional input of prey isotopic values, fractionation coefficient estimates, and prey elemental composition, the approximate proportions of the predator diet can be estimated through the use of isotope mixing models (Schwarcz 1991, Phillips 2001). The isotope mixing model used herein is designed to quantify the relative contributions of the pelagic/benthic food chains, to provide an indication of relative trophic positions, and to measure the trophic relationships between key organisms.

Three of the economically important groundfish species found along the Newfoundland and Labrador shelves are Atlantic cod (*Gadus morhua*), redfish (*Sebastes* sp.) and Greenland halibut (*Reinhardtius hippoglossoides*). Between 2013 and 2017 these three species represented 78.1% of the landed value of groundfish species in the

Newfoundland-Labrador region (DFO 2019). Given their relative importance to the fisheries in this region, several historical studies of their diets have been conducted using stomach contents analysis. The demersal Atlantic cod are thought to be primarily generalist feeders but do show preferences towards high-lipid forage fish such as capelin (e.g. Minet & Perodou 1978, Lilly 1991, Link & Garrison 2002, Krumsick & Rose 2012). The mostly pelagic redfish has been reported to feed primarily on pelagic invertebrates such as hyperiid amphipods, copepods, euphausiids, and northern shrimp (e.g. Lambert 1960, Pedersen & Riget 1993, González et al. 2000, Pérez-Rodríguez & Saborido-Rey 2012). The Greenland halibut, or turbot, is primarily a bottom fish but is thought to be an active mid-water predator. As such, their diet consists has been reported to consist of a wide variety of pelagic and demersal prey, particularly capelin, shrimp, squid, and zooplankton (e.g. Chumakov & Podrazhanskaya 1986, Bowering & Lilly 1992, Dawe et al. 1998, Dwyer et al. 2010). All of these diets have been reported to have changed along with the large-scale ecosystem changes that were observed in this region in the early 1990s (Rose & O'Drsicoll 2002, Dwyer et al. 2010, Pérez-Rodríguez & Saborido-Rey 2012).

Given the utility of stable isotope analyses to contribute new information on the structure of food webs and trophic dynamics among ecosystems, our objectives are threefold: (1) to construct simplified marine food webs based on results from stable isotope mixing models supplemented by information from stomach contents data for three regions within the northeast coast of Newfoundland and Labrador and then compare food web metrics among regions; (2) to analyze in greater detail spatial variation in the

diets of the three abundant and economically important species: Atlantic cod, redfish and Greenland halibut, and; (3) to discuss the isotope mixing model results in the context of recently reported spatial variation in marine fish ontogenetic niche overlap and size-spectrum recovery among regions.

Materials and Methods

Study Area

Sampling was undertaken within marine research surveys conducted by the Center for Fisheries Ecosystems Research (CFER) aboard the *RV Celtic Explorer* in May 2015 on the offshore shelves from southern Labrador and eastern Newfoundland, corresponding to Northwest Atlantic Fishery Organization (NAFO) subdivisions 2J, 3K, and 3L (Fig. 3.1). These subdivisions together represent the management unit for the 'Northern' Atlantic cod stock (Templeman 1979, Rose et al. 2000, Smedbol & Wroblewski 2002). Three major trenches or corridors within this region had previously been identified as important onshore-offshore cod migration pathways: Hawke Channel, Notre Dame Channel, and the Bonavista Corridor (Rose 1993) which were selected as the focal research regions. The following analyses were conducted within each region separately in order to quantify spatial variation.

Sample Collection

The collection of samples used for this study was reviewed and approved by the Memorial University Animal Care Committee under the guidelines set by the Canadian

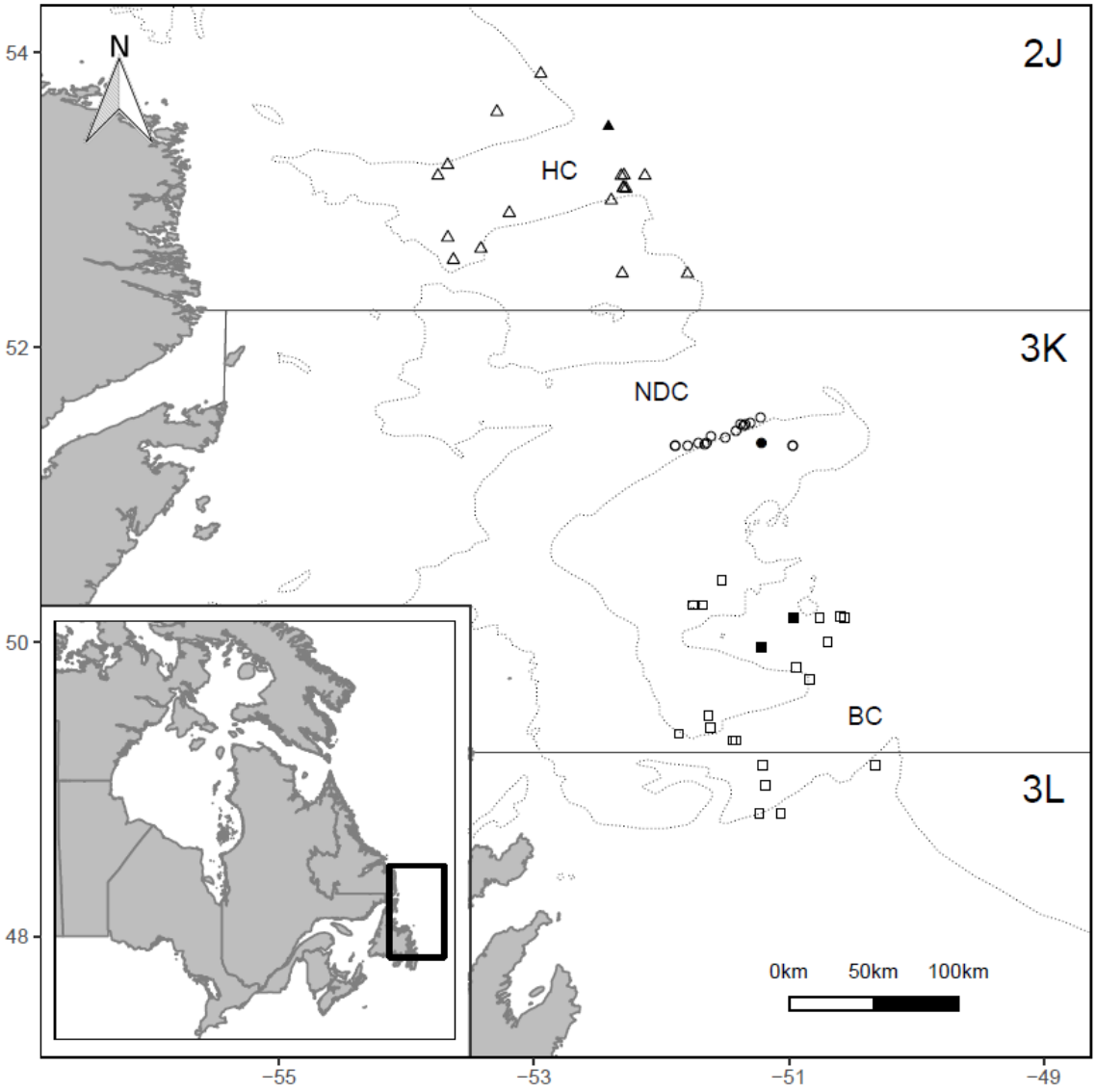


Fig. 3.1 Map of Newfoundland and southern Labrador with sampling locations. The trawl locations are indicated with open symbols and plankton tow locations with closed symbols for the Hawke Channel (HC, triangles), Notre Dame Channel (NDC, circles), and Bonavista Corridor (BC, squares). The inset map outlines the study domain in eastern Canada. The relevant NAFO subdivisions 2J, 3K, and 3L boundaries are also indicated. Dashed lines represent 300 m depth contours. The bathymetry map is reproduced from GEBCO world map 2014 (www.gebco.net) and NAFO subdivisions reproduced from NAFO (www.nafo.int).

Council of Animal Care. Samples were collected using a combination of Campelen 1800 and mid-water trawls (Chapter 2). All sets were deloyed between the hours of 7 am and 10 pm. In order to sample zooplankton, bongo nets (33 μm mesh and 60 cm diameter) were deployed obliquely within the surface layer for 10 minutes and at a speed of 2 knots. All fish caught in the trawl sets were sorted by species and standard lengths were recorded. The total biomass of each species was also assessed. In cases where a species was particularly abundant, subsampling was initiated involving 100 randomly sampled individuals. Dorsal muscle tissue samples were taken from all fish species with equal representation from the observed size ranges for each species. I sampled up to seven specimens within three length classes (small, medium, and large) for each species with the exception of species protected by the Species at Risk Act (Table 3.S1). For species with little variation in size (such as capelin and lanternfish), only nine specimens were collected within each region. From most fish, a transverse sample of dorsal muscle tissue directly posterior to the head was collected at-sea, placed in a 1.5 ml centrifuge vial and frozen at -20 ºC for stable isotope analyses. Stomachs were also collected at sea and preserved frozen. Stomachs from fish that showed signs of regurgitation or stomach eversion were not collected due to the potential of biasing stomach content results. The remaining fish with small, difficult to sample stomachs were individually labelled, bagged whole, and preserved frozen for dissection in the laboratory for their muscle tissue and stomachs.

While more species were caught and analyzed for their isotopic signatures (Table 3.S1), nine species represented the most abundant fish species: American plaice (*Hippoglossoides platessoides*), Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus harengus*), capelin (*Mallotus villosus*), checker eelpout (*Lycodes vahlii*), Greenland halibut (*Reinhardtius hippoglossoides*), lanternfish (N*otoscopelus* sp.), redfish (*Sebastes* sp.), and thorny skate (*Amblyraja radiata*). Based on the species' observed length distributions, sampled individuals were classified as small, medium, or large, by dividing the observed range of sizes into three length categories of equal width (Table 3.S2). These categories are recognized to be arbitrary, but as the exact timing of potential ontogenetic shifts was unknown, this division accounted for variation across the range of observed sizes. Of these, Atlantic cod, Greenland halibut, and redfish were selected to portray regional variability given their abundances and economic importance.

In addition to the fish samples, a variety of invertebrates were collected (Table 3.S1). Invertebrates were also sorted by species and measurements such as carapace width in crabs and carapace length in shrimp were obtained for up to 100 randomly sampled individuals. A sample of up to twenty-one of each invertebrate per region were frozen whole, with the exception of large snow crab, each of which was sampled by removing one leg. Zooplankton were collected from each plankton tow passed through through a 140 micron sieve and were preserved frozen for further taxonomical identification in the laboratory.

Stomach Content Analysis

Stomach samples were analyzed using a dissecting microscope and contents were identified to the lowest feasible taxonomic level. Individual weights and numbers of each prey taxa were quantified. From these measurements, in combination with their frequency of occurrence, the index of relative importance (IRI) was calculated for each prey taxa as follows:

$$IRI = \frac{\%N + \%B}{FO}$$

Where %N is the percent contribution of a given taxon to stomach content by numbers, %B is its percent contribution by weight, and FO is the frequency of occurrence, defined as the number of stomachs in which the prey taxon was detected over the total number of stomachs (Stevens *et al.* 1982). The percent IRI is presented as a percentage of the summation of the IRIs of all prey observed and were calculated for each predator species and region combination.

Stable Isotope Analysis

Muscle tissue samples were oven dried at 75°C for 48 hours and homogenized using an amalgamator. The homogenized samples were weighed, packaged in an airtight container with desiccant packages and shipped to the Cornell University Stable Isotope Laboratory (Ithaca, NY, USA) for analysis. Approximately 1 mg of sample was placed into 7×7 mm tin capsules, then flash combusted using a Carlo-Erba NC2500 elemental analyzer coupled on-line to a Finnigan MAT Delta Plus mass spectrometer for analyses of the resulting carbon dioxide and nitrogen gases.

Nitrogen and carbon ratios were expressed in delta (δ) notation, being the parts per thousand deviation from the standard material, Pee Dee belemnite limestone for carbon and atmospheric nitrogen for nitrogen, as follows:

$$\delta^{15}N \text{ or } \delta^{13}C = \left(\left(\frac{-R_{sample}-}{R_{standard}}\right) - 1\right) \times 1000 \quad (2)$$

$$R = {}^{13}C/{}^{12}C \text{ or } {}^{15}N/{}^{14}N \quad (3)$$

Lipids were not removed to avoid the potential influence of derived products on isotopic signatures (Pinnegar & Polunin 1999, Sotiropoulos *et al.* 2004, Logan *et al.* 2008). Therefore, following analysis, the δ^{13}C values were normalized for lipid bias as recommended by Ricklefs & Travis (1980) and Post *et al.* (2007), as follows:

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C{:}N \quad (4)$$

As the majority of fish samples were close to a C:N ratio of 3.3 as would be expected for muscle tissue of marine fish (Ricklefs & Travis 1980), this adjustment was only particularly relevant for lipid rich fish such as capelin, lanternfish and Greenland halibut.

Isotope Mixing Model

Although stomach contents provide detailed information on the diet composition of species, it represents the diet on the scale of hours to days (Eliott & Persson 1978, Jobling 1981, Temming & Herrmann 2003). In order to assess longer-term prey consumption and food web connections on the scale of months, we analyzed the diets of every caught predatory fish species using isotope mixing models. These models approximate the contributions of different prey while assessing their locations in isotope space relative to

adjusted predator values. These techniques are partly informed by priors, in our case stomach content data. Species or functional groups were further divided into four categories based on descriptions provided by Sherwood & Rose (2005) and Scott & Scott (1988) (Table 3.S1): benthic invertebrates, pelagic invertebrates, demersal fish, and pelagic fish. Some species, such as copepod species, were not found to differ in their isotopic signature and therefore were pooled together as a single functional group.

A fractionation coefficient, or discrimination factor, is the change in the isotopic signature from prey to predator that occurs due to partitioning upon consumption and assimilation of respective elements. Determining the exact fractionation coefficients between the predator and each individual food source is often recommended for each element (Caut *et al.* 2009). Such determination of prey-specific fractionation coefficients, however, was not possible in the present study. Historically a nitrogen fractionation of 3.4 has been used in ecological studies of fish populations and 0 for carbon, as if fractionation was assumed to be negligible (DeNiro & Epstein 1978, Fry & Sherr 1984, Minagawa & Wada 1984). However, these carbon estimates may have been underestimated and nitrogen overestimated (Barnes *et al*. 2007). As a result, two approaches were taken to estimate these discrimination factors. The coefficient was first estimated from the combination of stomach content analysis and the associated isotopic values of prey per Sherwood and Rose (2005). The bounds of values were 1.4 - 4.4 for nitrogen and -0.5 – 2 for carbon, as determined by biologically feasible fractionation coefficients (Hansson *et al.* 1997, Vander Zanden *et al*. 2001, Post 2002, McCutchan *et al.* 2003, Barnes *et al.* 2007, Caut *et al.* 2009, Hussey *et al*. 2010, Varela *et al.* 2011). For

estimated coefficients outside these bounds, the fractionation was estimated to be 3.4 for nitrogen and 0.4 for carbon (Post 2002).

Potential prey items to input into the mixing model were selected through a combination of the results of these stomach contents and published reports of North Atlantic diets (Table 3.S3). For species with particularly diverse diets, such as Atlantic cod and thorny skate, prey that represented over 5% of the weight and/or numbers were analyzed separately and all other reported prey items were combined into four functional groups (Table 3.S1): pelagic invertebrates, benthic invertebrates, pelagic fish and demersal fish. To acknowledge that any predator is gape-limited, only prey that were less than 24% of the predator's body mass were included in the model (Barnes *et al.* 2010). As not all individual weights were obtained, length-weight relations were used to determine approximate body masses for both predators and potential prey (Table 3.S4). For individual invertebrates which did not have size information, average species sizes were used.

The stable isotope mixing model to determine the percentage of the diets represented by key prey species was implemented using the MixSIAR package in R (Stock *et al.* 2018). Three basic equations were utilized in the Bayesian isotope mixing model to determine the proportions of the diet occupied by each prey type (Phillips & Koch 2002):

$$(\delta^{13}C_1 - \delta^{13}C_M)[C]_1 f_{1,B} + (\delta^{13}C_2 - \delta^{13}C_M)[C]_2 f_{y,B} + \cdots + (\delta^{13}C_n - \delta^{13}C_M)[C]_n f_{n,B} = 0 \quad (5)$$

$$(\delta^{15}N_1 - \delta^{15}N_M)[N]_1 f_{1,B} + (\delta^{15}N_2 - \delta^{15}N_M)[N]_2 f_{2,B} + \cdots + (\delta^{15}N_n - \delta^{15}N_M)[N]_n f_{n,B} = 0 \quad (6)$$

$$f_{1,B} + f_{2,B} + \cdots + f_{n,B} = 1 \quad (7)$$

Where $\delta^{13}C_n/\delta^{15}N_n$ represent the tissue isotopic values for a given prey item, $\delta^{13}C_M/\delta^{15}N_M$ the tissue isotopic values for the predator, $[C]_n$ the carbon concentration of a given prey, $[N]_n$ the nitrogen concentration of a given prey, and $f_{n,B}$ the proportion of the predator's diet represented by the given prey species. Size category (small, medium, or large) was included as a fixed variable for species-region combinations that demonstrated ontogenetic variation. Region- and species-specific IRIs calculated within this study were provided as a prior to these mixing models (Moore and Semmens, 2008). Some species-region combinations did not contain stomach data due to a high percentage of empty stomachs. In these few cases, an average IRI from other available regions was used. For cases where there are three or fewer potential prey sources, this model is able to provide exact contributions to the predator's diet of each prey. For greater than three potential prey sources, fifty thousand repetitions of the mixing model were run to determine the approximate proportion of the diet each prey taxon occupies.

Food Web Metrics

Several food web metrics were calculated to characterize the three constructed food webs. The total number of "nodes" or functional groups represents the network size. The "connectance" of the food web is the fraction of all possible predatory links that are realized and the ratio of trophic links within the food web over the square of the network size (Martinez 1992, Warren 1994). For each species, a number of metrics were calculated to determine the importance of each prey. The "number of links per node"

represents the number of predators feeding on that prey. The "average percent of predator diets" is the mean percentage of a given prey within the linked predator diets. The "relative link strength" is calculated as the sum of all the diet proportions contributed by a given prey taxon over the total summation of diet proportions for all food web links within a given region. Ellipses enclosing benthic invertebrates, demersal fish, pelagic invertebrates and pelagic fish in isotopic biplot space were estimated using the Khachiyan algorithm for the computation of minimum volume enclosing ellipsoids (Khachiyan 1979).

From the outcomes of the isotope mixing models and these food web metrics, I constructed simplified food webs for the predatory fish species. Within isotope biplot space, all of the species were plotted with species showing ontogenetic variability in their isotopic signatures represented as a maximum of three points. Links between predatory species and their respective prey, identified through our stomach content analyses and reported predation in the literature, were plotted with the line width proportional to the importance to the predator's diet. The proportion of the total linkage strength for each prey item as determined by summing all of the linkage strengths from the prey item and dividing by the sum of all linkage strengths determined within the food web. A circle was drawn over the respective prey items in biplot space whose radius was proportional to the size of these total linkage strengths to indicate the relative importance of prey species as conduits of energy flow into the upper food web.

Results

Index of Relative Importance

Stomach content data from all fish species were collected to use as priors for the stable isotope mixing model. From the stomach contents alone, half of the percent IRIs of the three focus fish are made up of shrimp, snow crab, hyperiids, and capelin (Table 3.1, Table 3.S5). Shrimp consumption increased with latitude, representing an average of 19.2% IRI in the Bonavista corridor and increasing to 33.4% in the Hawke Channel. Gammarids were also a common prey item of Hawke Channel fish, representing an average of 13.3% IRI. Pelagic invertebrates were found to be a dominant prey item in the Notre Dame Channel representing 58.6% IRI, particularly hyperiids and copepods representing an average 26.0% and 31.5% IRI. The Bonavista Corridor was noted to have increased incidence of crab (8.5% IRI), polychaetes (16.7%), and pelagic fish (particularly capelin; 4.3%).

Simplified Food Web Model

The most nitrogen depleted values were observed in the pelagic algae and benthic plant material (Fig 3.2) and the highest trophic level species was the Atlantic cod. While the pelagic components of the ecosystem fell within a relatively small range of δ^{13}C values, the benthic community was found to exhibit a wide spread of δ^{13}C values (Fig 3.2). Within the benthic component of the food web invertebrates, particularly echinoderms, exhibited a larger range of carbon values than the fish species.

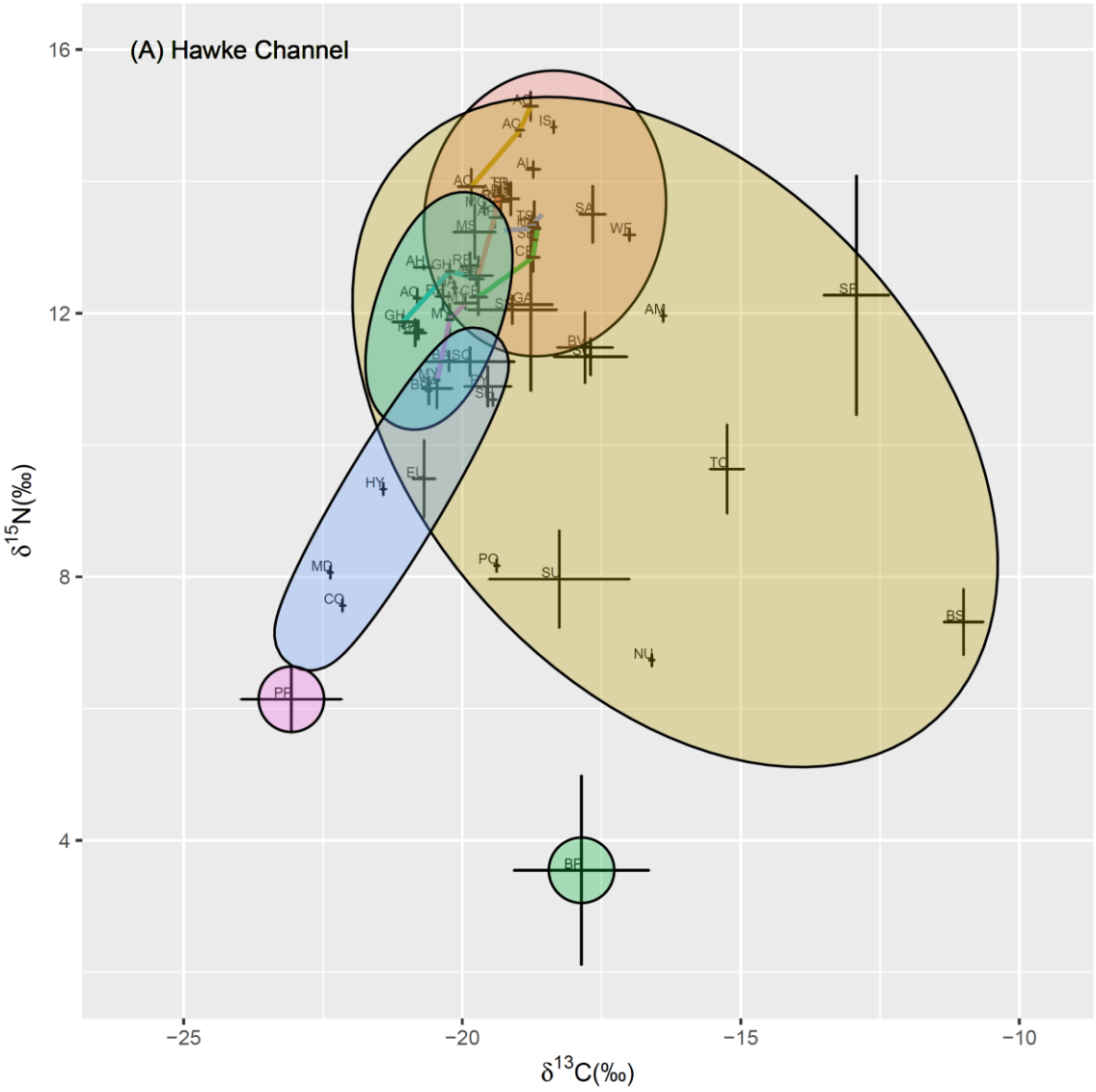
Table 3.1 Diet composition of three highlighted predatory fish species presented as a percent index of relative importance (IRI) divided by region. A fractionation coefficient was estimated from this stomach contents data to use in the isotope mixing model.

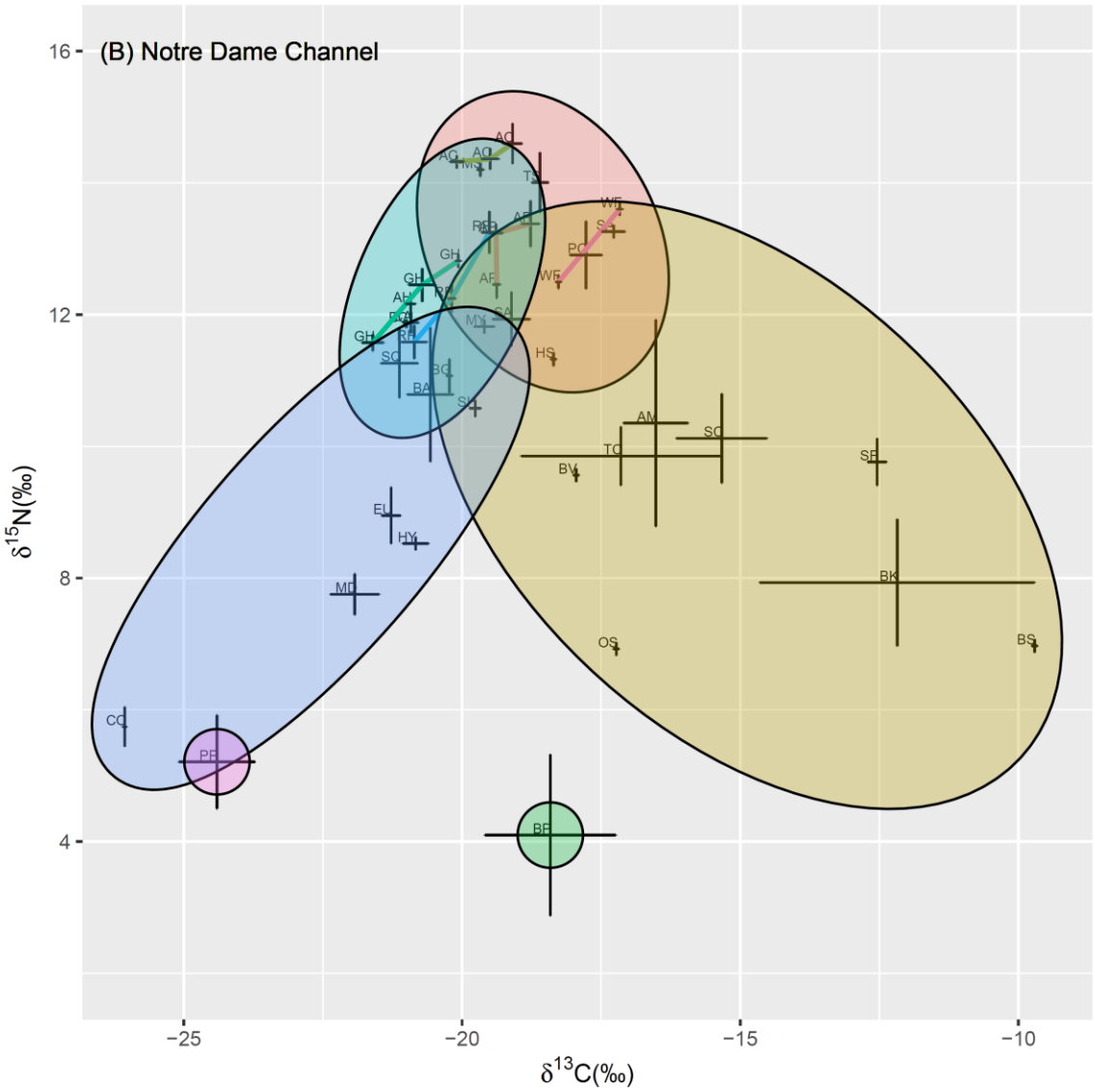
Species	Fractionation Coefficient	Region	Prey species
Atlantic Cod	3.9 / -0.4	HC	Shrimp (72.2%), Demersal Fish (25.3%), Other Benthic Invertebrates (2.5%)
		NDC	Shrimp (98.4%), Snow Crab (0.4%), Hyperiid (0.3%), Demersal Fish (0.3%), Benthic Invertebrates (0.3%), Euphausiid (0.2%), Polychaete (0.1%)
		BC	Snow Crab (43.9%), Benthic Invertebrates (38.7%), Shrimp (11.9%), Polychaete (1.6%), Demersal Fish (1.6%), Checker Eelpout (1.0%), Hyperiid (0.8%), Pelagic Fish (0.5%)
Greenland Halibut	3.4 / 0.4	HC	Shrimp (73.1%), Gammarid (10.7%), Demersal Fish (8.0%), Benthic Invertebrates (3.9%), Copepod (1.7%), Capelin (0.4%), Pelagic Invertebrates (0.4%)
		NDC	Hyperiid (99.7%), Gammarid (0.1%), Shrimp (0.1%)
		BC	Capelin (82.9%), Shrimp (10.1%), Hyperiid (2.7%), Checker Eelpout (1.3%), Copepod (1.2%), Benthic Invertebrates (1.2%), Redfish (0.4%), Gammarid (0.3%)
Redfish	3.4 / 0.4	HC	Shrimp (76.3%), Copepod (14.7%), Hyperiid (5.5%), Euphausiid (2.0%), Capelin (1.0%), Benthic Invertebrates (0.4%)
		NDC	Shrimp (81.5%), Copepod (11.1%), Mysid (3.9%), Capelin (2.3%), Euphausiid (1.2%)
		BC	Shrimp (77.4%), Hyperiid (12.3%), Copepod (8.0%), Euphausiid (1.0%), Capelin (0.9%), Mysid (0.3%), Benthic Invertebrates (0.1%)

Table 3.2 Three food web metrics calculated for the food webs in each region.

Region	Network Size	Links per Species	Connectance
Hawke Channel	42	4.40	0.105
Notre Dame Channel	31	3.94	0.127
Bonavista Corridor	43	3.93	0.091

The food web for the Newfoundland and Labrador shelf regions, even when simplified, displayed numerous linkages (Fig. 3.3). Each ecosystem consisted of between 31 and 43 observed trophic "nodes" with the Notre Dame Channel likely lower due to less intensive sampling (Table 3.3). However we also observed at the highest latitude system an ~10% increase in the number of links per prey species (Table 3.2), which is associated with the increased connectance in the two northern regions. Strong latitudinal increases were observed in the linkage strength of shrimp, more than doubling from 0.105 to 0.264 and PPD increasing from 21.2 to 38.1, and squid, which was only found to be a major part of some species diets in the Hawke Channel. Meanwhile, prey such as copepods (LS increasing from 0.135 to 0.216, PPD from 14.8 to 24), brittle stars (LS increasing from 0.021 to 0.050, PPD from 4.8 to 12) and fish species were more frequently consumed in the southern regions (Fig 3.3). The Notre Dame Channel also saw a spikes in prey items from the center of the biplot space such as hyperiids (LS of 0.297, PPD of 37.3) and bivalves (LS of 0.098, PPD of 27.7).


(A) Hawke Channel
16
12
8
4
−25
−20
−15
−10
δ15N(‰)
δ13C(‰)
SA
WE
SE
AM
BV
TO
PQ
SL
BS
NU
HY
EU
MD
CO
PE
BE


(B) Notre Dame Channel
16
12
8
4
δ^{15}N(‰)
−25
−20
−15
−10
δ^{13}C(‰)
AC
AG
AQ
MS
TS
WE
SA
PC
GH
AF
AH
RE
MY
HS
SC
BC
BA
SK
AM
SQ
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BR

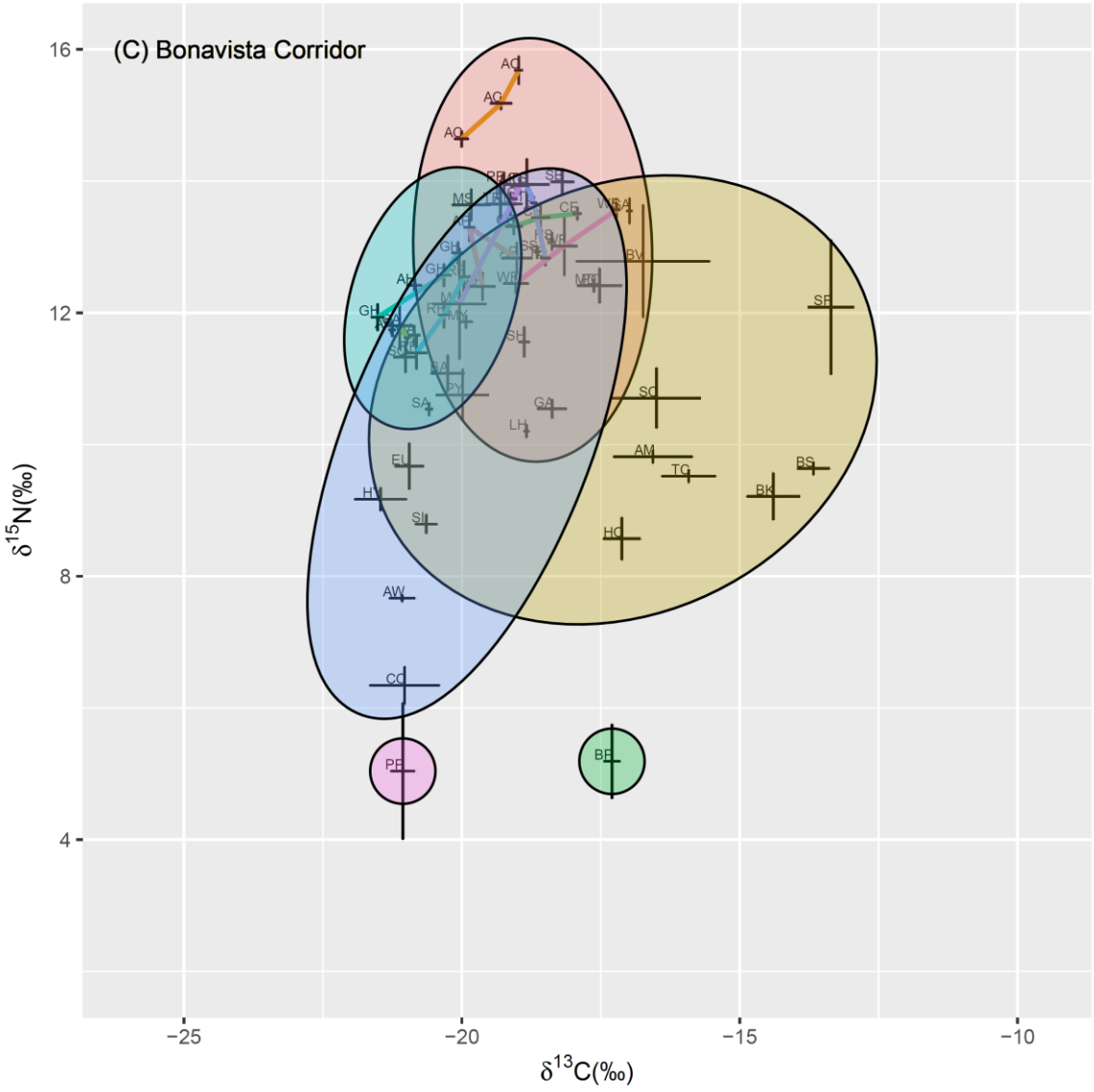
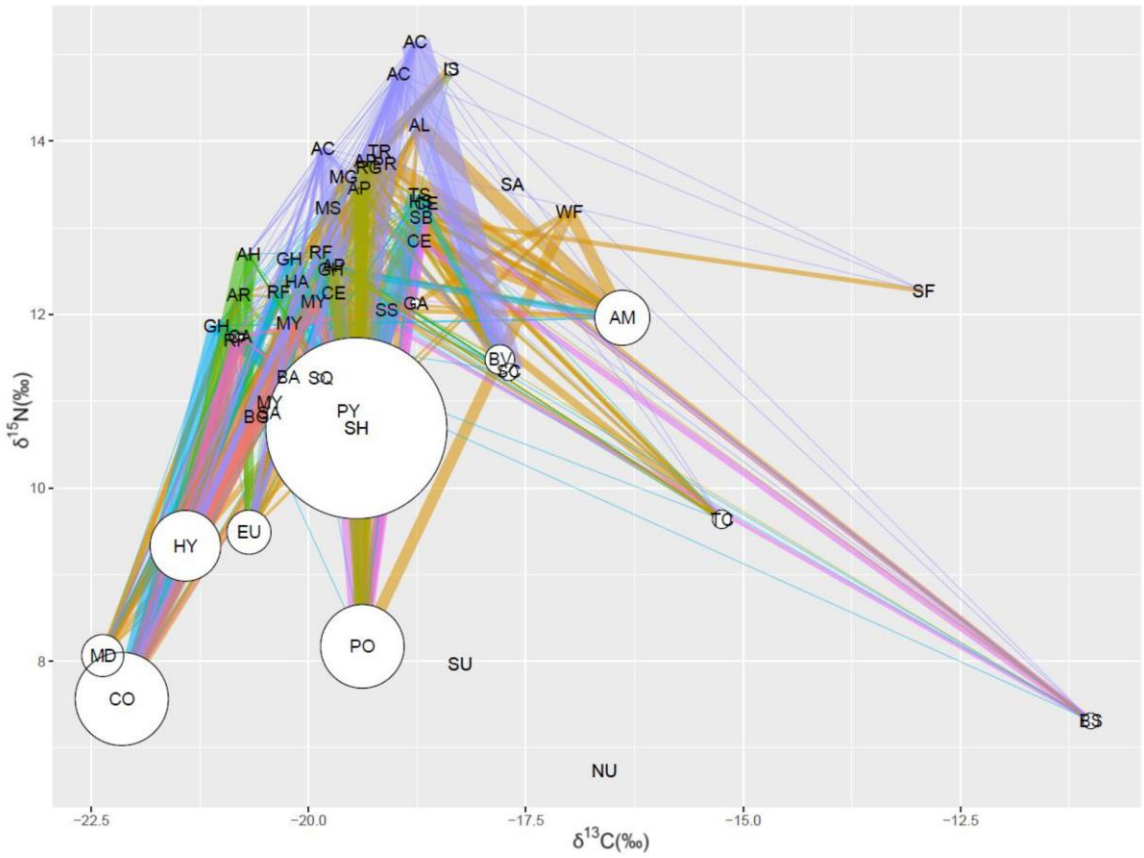
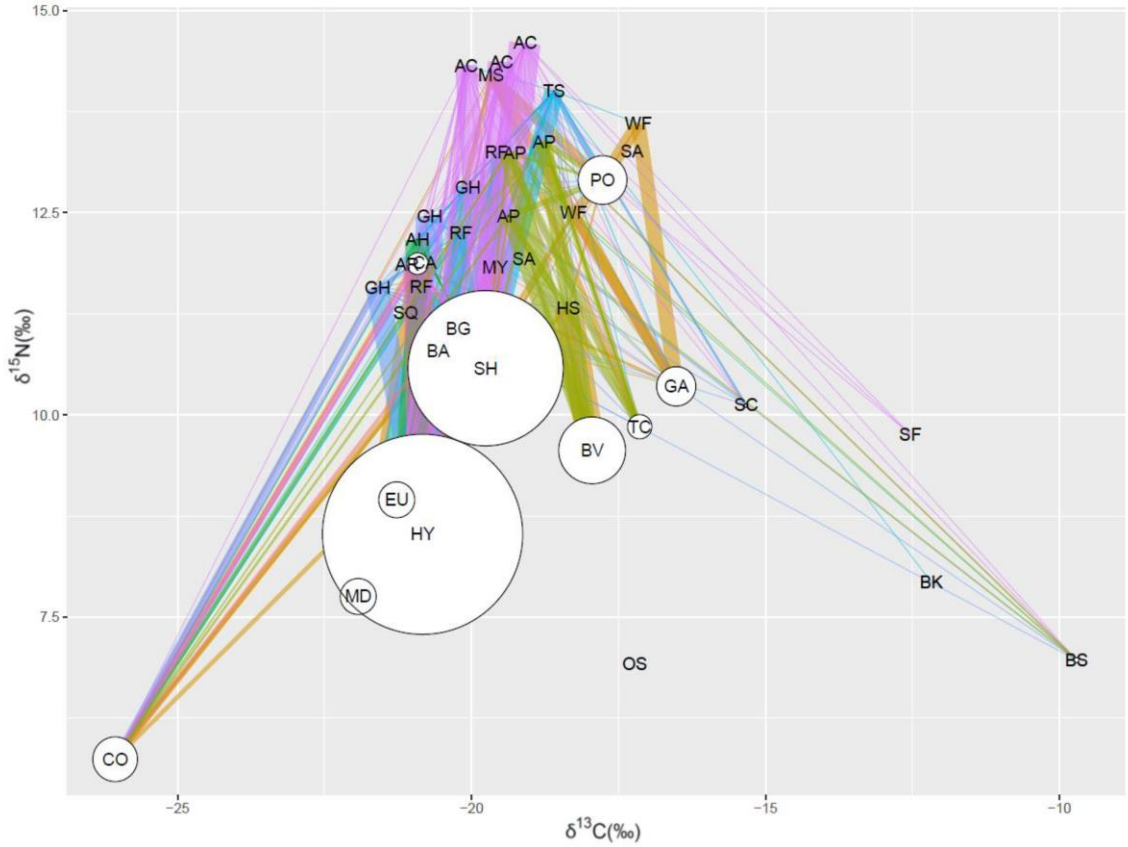


Fig. 3.2 Stable carbon and nitrogen isotope values (mean ±SE) of pelagic (blue oval) and benthic (peach) components of the food webs in (A) the Hawke Channel, (B) the Notre Dame Channel, and (C) the Bonavista Corridor. In cases where a species demonstrated ontogenetic variation in their isotopic signatures, these species are represented by three points connected by linear lines. Species abbreviations are defined in Table 3.S1.

(A) Hawke Channel



(B) Notre Dame Channel



(C) Bonavisata Corridor

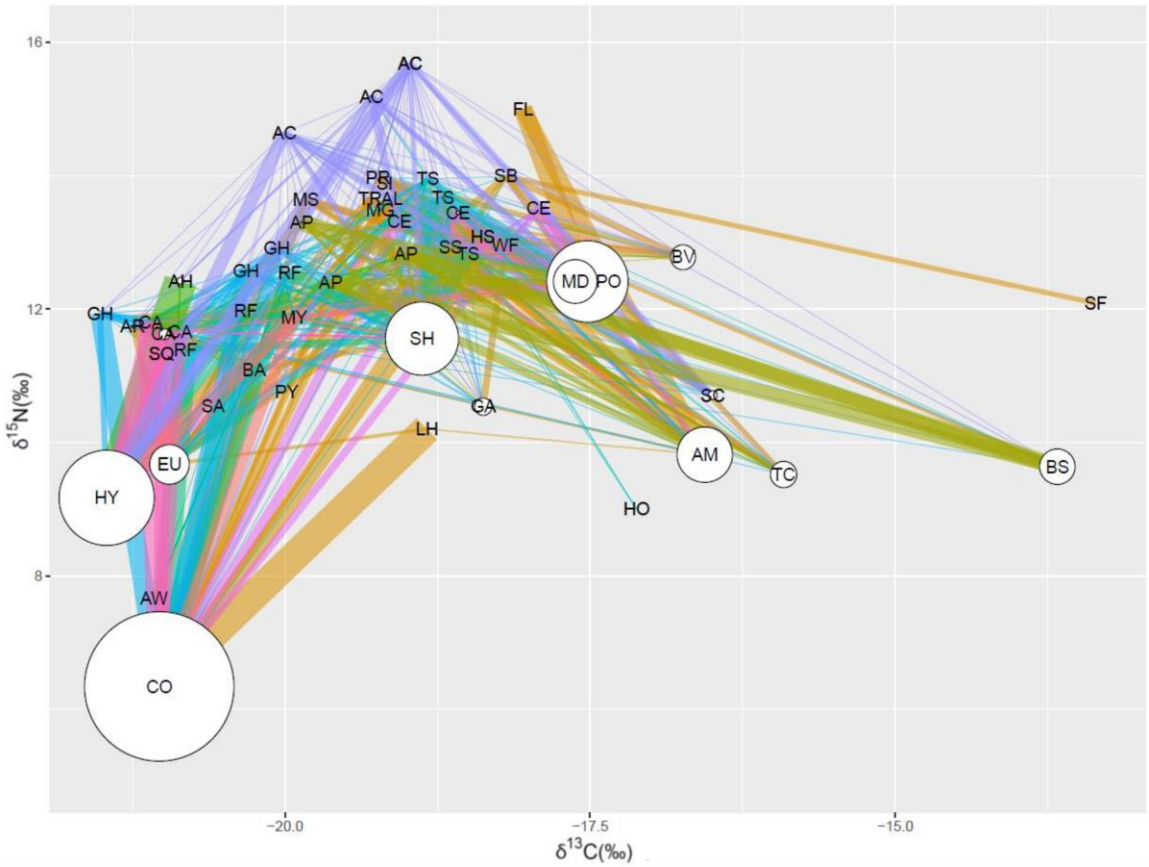


Fig. 3.3 Simplified food web with line widths indicating the strength of the predatory interaction for (A) the Hawke Channel, (B) the Notre Dame Channel and (C) the Bonavista Corridor. Circles represent the relative link strength from the given prey species. Species from which a number of size classes were obtained will appear up to three times (for small, medium, and large size categories). Taxa abbreviations are defined in Table 3.S1.

Table 3.3 Food web link characteristics for the three focus regions. #L (Number of Links) represents the number of predators preying on that species/group. LS represents relative link strength which is calculated as the sum of all the diet proportions contributed by a given prey taxon over the total summation of diet proportions for all food web links within a given region. For each prey species, the percent of each linked predator diet represented by that prey was averaged as PPD (average percent of predator diet).

Prey Species	Bonavista Corridor			Notre Dame Channel			Hawke Channel		
	#L	LS	PPD	#L	LS	PPD	#L	LS	PPD
American Plaice	3	0.001	1.4	4	0.001	1.7	0	0	0
Arctic Cod	9	0.002	3.2	0	0	0	0	0	0
Atlantic Cod	8	0.001	1.0	0	0	0	0	0	0
Atlantic Herring	14	0.008	1.2	0	0	0	0	0	0
Bivalve	20	0.034	10.1	13	0.098	27.7	19	0.041	10.7
Brittle Star	13	0.050	14.8	12	0.006	1.4	17	0.021	4.8
Capelin	31	0.014	7.6	14	0.030	6.2	14	0.010	3.9
Checker Eelpout	3	0.004	0.3	0	0	0	0	0	0
Copepod	33	0.216	31.9	24	0.065	6.9	34	0.135	14.8
Euphausiid	31	0.056	10.7	23	0.052	7.8	29	0.063	8.0
Gammarid	34	0.079	11.7	21	0.057	8.6	31	0.079	10.9
Gastropod	16	0.023	6.9	0	0	0	12	0.012	3.7
Greenland Halibut	6	0.001	2.1	0	0	0	0	0	0
Hyperiid	32	0.137	25.1	22	0.297	37.3	24	0.102	17.4
Isopod	0	0	0	0	0	0	11	0.016	7.4
Marlinspike	6	0.001	2.0	0	0	0	0	0	0
Myctophiid	13	0.001	2.5	0	0	0	0	0	0
Mysid	30	0.062	13.2	23	0.052	10.6	35	0.060	6.1
Polychaete	30	0.117	17.2	18	0.071	11.4	26	0.121	18.3
Shrimp	30	0.105	21.2	20	0.230	28.9	28	0.264	38.1
Snow Crab	13	0.011	10.1	13	0.004	2.1	14	0.023	7.5
Squid	0	0	0	0	0	0.2	10	0.009	3.7
Thorny Skate	3	0.001	2.1	0	0	0	0	0	0
Toad Crab	16	0.036	8.7	11	0.034	6.9	15	0.025	5.3

Trends Among Three Focus Species

While a variety of predatory fishes were analyzed as part of this study, I chose to focus on three abundant and economically important species. For details on additional abundant species, refer to Figs 3.S1-3.S6.

Within Atlantic cod diets, in the BC, 75% consisted of shrimp, snow crab, polychaetes, hyperiids and benthic invertebrates; in the NDC: shrimp and hyperiids; in HC: shrimp, snow crab, euphausiids, and pelagic invertebrates (Fig 3.4). Across all three regions shrimp made up a quite substantial portion of cod diets increasing in the northern regions. With increasing size we observe the contribution of zooplankton to the

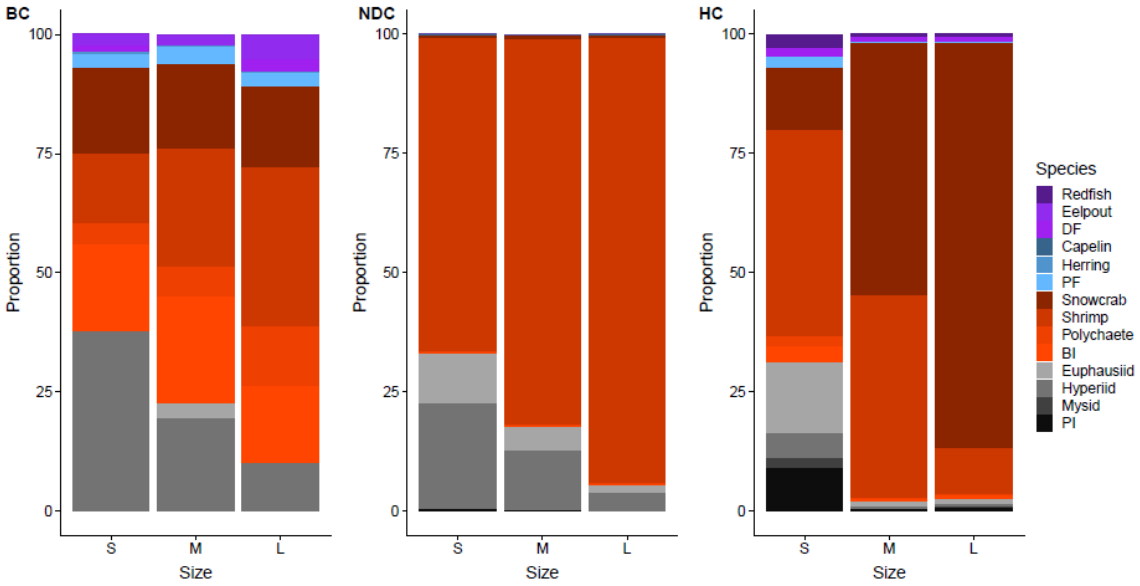


Fig. 3.4 Atlantic cod diet composition as determined from isotope mixing models divided by size category (S for small, M for medium, L for large) and region (BC for Bonavista Corridor, NDC for Notre Dame Channel, HC for Hawke Channel).

diet decreases and is replaced with benthic prey. Furthermore, snow crab, another economically important species in the region, was observed to make up quite a substantial portion of the diet in the Bonavista Corridor and dominate cod diets within the Hawke Channel (Fig 3.4). Demersal and pelagic fish make up a small portion of the diet in the Bonavista Corridor that was found to decrease in the other two regions.

Greenland halibut is another economically important species that currently provides the highest groundfish landings value in the Newfoundland and Labrador region. In the Bonavista Corridor the diet of this fish was comprised mostly of copepods with generous contributions from hyperiids and capelin (Fig 3.5). The Notre Dame Channel saw a shift from a copepod-dominated diet to one comprised primarily of hyperiids. Once again,

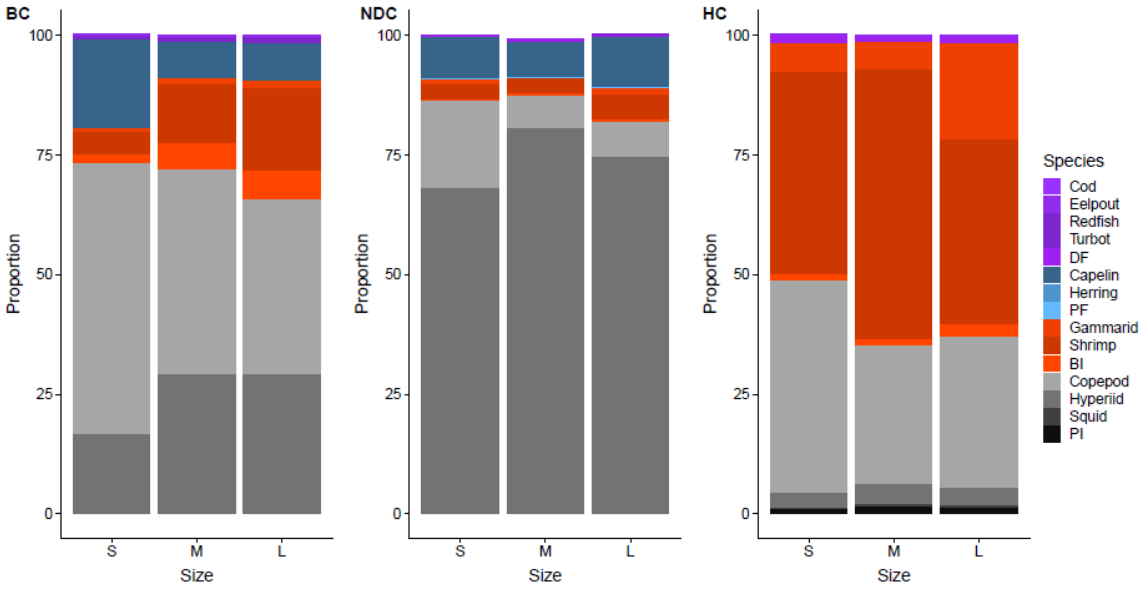


Fig 3.5 Greenland halibut diet composition as determined from isotope mixing models divided by size category (S for small, M for medium, L for large) and region (BC for Bonavista Corridor, NDC for Notre Dame Channel, HC for Hawke Channel).

shrimp dominated the Hawke Channel diets. With increasing size we observed a decrease in zooplankton consumption.

Redfish diets were relatively less complex in comparison to the previous two diets, consisting of mostly zooplankton and shrimp (Fig 3.6). The relative proportions of these two contributions were found to vary across regions with a steadily increasing contribution of shrimp with increasing latitude. Increases in shrimp consumption was also observed with ontogeny across all regions.

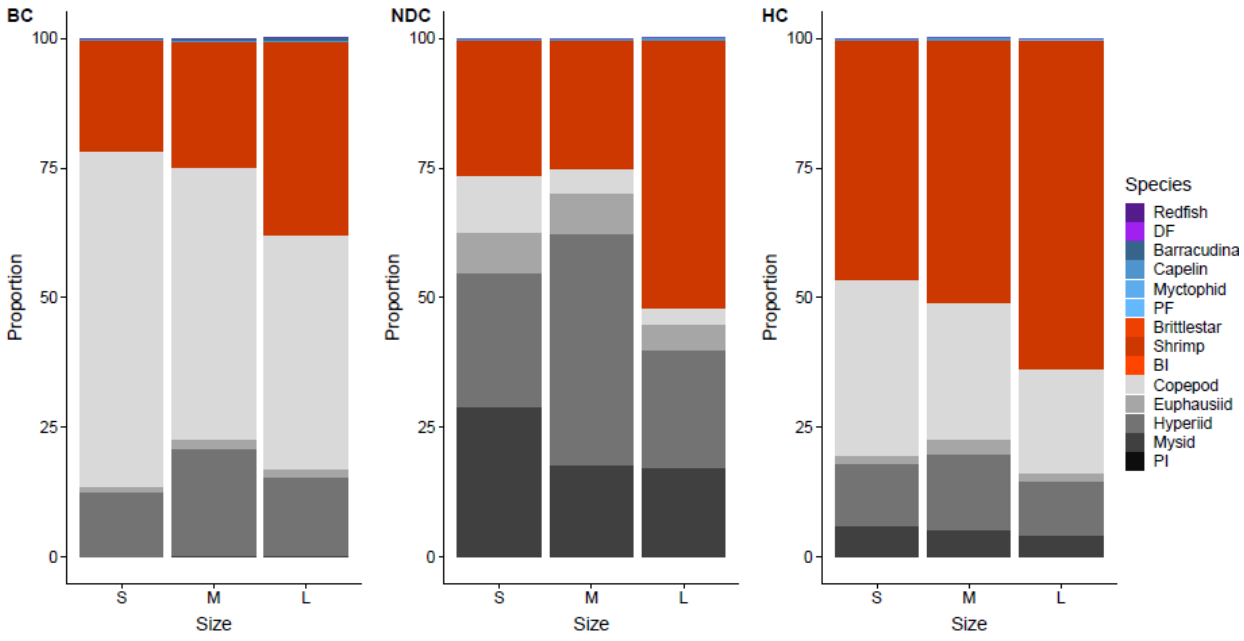


Fig. 3.6 Redfish diet composition as determined from isotope mixing models divided by size category (S for small, M for medium, L for large) and region (BC for Bonavista Corridor, NDC for Notre Dame Channel, HC for Hawke Channel).

Discussion

I report the results of within- and among-region variation in the Newfoundland and Labrador shelf marine ecosystem analyzed using isotope mixing models to examine whether regional variation in community overlap (Chapter 2) and differential size-based community recovery rates (Chapter 4) may be explained by differences in energy and nutrient flows through ecosystems recovering from overexploitation (Pedersen et al. 2017).

Stable isotope ecology has proven to be an effective means of assessing such flows as it directly attempts to track the path of rarer heavier atoms through the food web (Fry 2006, Parnell et al. 2013, Phillips et al. 2014). In addition to helping to identify and quantify key trophic interactions within the ecosystem, particularly robust to spatial variation in the importance of shrimp among regions, stable isotopes also provided insights into the underlying processes that are governing these ecosystems by resolving the relative importance of the pelagic and benthic components of the community. To demonstrate the importance of considering this regional variability in species interactions, I highlighted the regional variation in reconstructed diets observed in three economically important groundfish species.

While in the invertebrates we observe extremes in the carbon values, indicating a strongly pelagic or a strongly benthic signature, the fish species tended towards a central carbon isotope value. This tendency towards centrality tends to became more pronounced with increasing size, suggesting a balance between the exploitation of pelagic and benthic productivity. The balanced acquisition of pelagic and demersal productivity has recently

been hypothesized to explain the dominance of large benthic demersal fishes over large pelagic fishes in boreal and temperate regions (van Denderen et al. 2018). Whether this energy acquisition hypothesis also influences ecosystem recovery is a related question with potential implications for differential ecosystem recovery pathways. For example, recoveries of community size-structure are strongest in the Bonavista Corridor compared to the other two regions (Chapter 4). Given both this hypothesis and our reported patterns, further examinations of benthic-pelagic prey contributions to predator diets should be included in analyses of differential recovery of marine ecosystems.

Many of the known detritivore invertebrates have been noted to have relatively enriched carbon signatures. This finding is consistent with the results found in other studies (Hobson et al. 2002, Nadon & Himmelman 2006). I was not able to obtain isotopic values for the detritus, but we may infer this food source would possess a more enriched nitrogen and carbon signature compared to the benthic plant material in order to account for the wide range of values in the benthic portion of the community (Schlacher & Wooldridge 1996, Wooler et al. 2003, Tewfik et al. 2005).

To further explain benthic and pelagic differences in prey consumption among regions, each region was characterized by a few key prey species as revealed by the link strength between predators and prey in the food web models. The diets in the Bonavista Corridor are known to be the most diverse of these three regions from previous published research (Krumsick & Rose 2012, Chapter 2). This study further demonstrated that groundfish in this region show increased consumption of a variety of fish species (many of them pelagic forage fish), copepods, and brittle stars. With the exception of the

increased copepod and brittle star consumption, these observations result in overall higher trophic level of the top-level predators and facilitate strong contributions of both the pelagic and benthic portions of the food webs towards generalist feeders. The Notre Dame Channel was characterized by important prey species found in the middle of the food web: bivalves and hyperiids. Extreme carbon values were observed in this region among copepods and echinoderms. I presently lack an explanation for these extreme values. The stable isotope and the stomach content data, however, consistently demonstrated the importance of zooplankton and infauna to the diets of fish in this region. Finally, the Hawke channel food web was dominated by the consumption of shrimp, although squid consumption was also found to be relatively higher in this region even if it only comprised a small portion of the diet. Although squid population estimates for the northern regions have not been published, squid catches and abundance estimates were low in 2015 (Hendrickson & Showell 2016). The vast majority of species in this region were found to at least have shrimp in their stomach contents if not representing the majority of the contents, consistent with numerous other groundfish diet studies in this region (e.g. Bowering et al. 1983, Parsons 2007, Krumsick & Rose 2012).

Three abundant fish species of socioeconomic importance were analyzed in greater detail due to recent debates regarding their population status and interactions with other fisheries. The biomass of these predators is often greater in the southern region studies than the north (Healey 2010, DFO 2011, DFO 2018, Rose & Rowe 2018) and represented the most abundant species caught in our bottom trawls (Chapter 2, Chapter 4). I observed that shrimp and/or crab often comprised a substantial portion of the diet with the

proportion increasing with ontogeny (Figs 3.4-3.6). Additionally, as northern regions show less diversity in diet and fish communities (Chapter 2), shrimp and crab become increasingly important channels of nutrient flow through the food web. Shrimp and crab currently represent the two most economically dominant fisheries within the Newfoundland and Labrador region, with landed values of $222 million and $295 million, respectively. These values greatly exceed the recent landed values of Atlantic cod ($23 million), redfish ($11 million), and turbot ($57 million) (DFLR 2018). Thus, while shrimp and crab are presently the two most lucrative fisheries they also represent major prey for these groundfish species (e.g. Lilly et al. 2000, Worm & Myers 2003, Mullowney et al. 2014), the impact of which depends on the respective species- and size-specific predator population sizes. Given these food-web links, demersal fish recovery would therefore likely negatively impact the present shellfish industries.

A number of food web metrics were presented in order to better quantify these communities. The network size was found to be similar in the Hawke Channel and the Bonavista Corridor, though lower in the Notre Dame Channel. It remains unclear whether this reduced network size in the Notre Dame Channel was a relic of less sampling effort or a result of an underlying biological process. Analysis of stomach contents indicated that a number of benthic invertebrates were not sampled with our trawl gear, suggesting that the Notre Dame Channel likely has a larger network size. Inclusion of these unsampled nodes (a total of 6), however, does not increase the network size to those observed in the Hawke Channel or Bonavista Corridor. I observed that between the Bonavista Corridor and the northern regions there was a distinct increase in the

connectance. This increase is associated with decreased food chain lengths (Williams et al. 2002). Food webs also tend to be shorter in systems characterized by high predator-prey mass ratios (PPMR) (Jennings & Warr 2003). The observation that fish consumption tends to be reduced in the northern regions while zooplankton and shrimp become a much more prominent part of the diet would explain these observations, and the finding that PPMR is much higher in the Hawke Channel than other regions (Chapter 4). The links per prey species were found to be greater in the northern regions. Given these regions show lower diversity, predators would be expected to be more likely to prey upon common species. This metric therefore confirms that food web complexity decreases with latitude. This food web metric, however, has been called into question as it has been noted to incorrectly characterize ecological trends when varying number of nodes are present between food webs (Havens 1992). Despite this caveat, we observe the largest difference between the two regions with comparable network size, indicating an underlying ecological process may be responsible for the observations.

Numerous limitations exist when constructing these isotope mixing models. Firstly, an assumption was made that all potential prey species are represented within the model. The survey gear types utilized naturally limited the species and the size ranges used in this study, and as such there are undoubtedly going to be some gaps that are not represented by the available samples. A striking example of this is the absence of detritus in the analysis. As I did not have access to a grab sample, the detritus that undoubtedly makes up a major component within the food web needed to be left out. We could infer the approximate position within biplot space based on the positions of the detritivores,

but given the wide range of carbon and nitrogen isotope values among these detritivores we cannot conclusively state the exact range of detrital isotopic values. Other key components to the food web that are missing are the birds and marine mammals that could not be sampled given the presented methods. To account for such omissions, I present a simplified food web based on the species and prey that were caught as opposed to a complete food web that would account for such key components.

Most taxa that were identified in the stomachs had representative isotopic values from the trawl data. While all of the major taxa present within the stomachs (representing > 5% of the Atlantic cod stomach contents by weight), minor invertebrate taxa were sometimes not represented in the isotopic signature. The Bonavista Corridor was missing sea cucumbers (3.4% of cod stomach content biomass); Notre Dame Channel was missing gastropods, crabs (*Cancer* sp.), tunicates, bryozoans and sea urchins (all at less than 0.1% of cod and Greenland halibut stomach content biomass); and Hawke Channel was missing sipunculids (0.1% of American Plaice stomach content biomass) and bryozoans (0.01% of cod stomach content biomass). Given the limitations of trawl sampling on invertebrate communities, it is not unexpected to be missing taxa. The only fish species that was found in a stomach that was not observed in the trawl catches were grenadiers in the Notre Dame Channel (0.3% of stomach content biomass). With the exception of gastropods, all of the before mentioned taxa would have been grouped in either "other benthic invertebrates" or "other demersal fish" categories. Since these underrepresented species occurred infrequently in limited quantities, it appears unlikely that their omission would impact the results of the isotope mixing model. I also chose not to sample these

taxa from the stomachs themselves as digestion has been shown to influence isotopic compositions (Hwang et al. 2007, Guelinckx et al. 2008). The stomach contents were also used in combination with those from other published studies as a means of determining potential prey as inputs for the stable isotope mixing model. However, this choice in methods does lend itself to uncertainty regarding the detectability of different prey (Baker et al. 2013). For example, prey types will have variable evacuation rates which could bias the results of stomach contents analysis (Rindorf & Lewy 2004). Combining this analysis with stable isotope analysis helps to resolve this bias. An alternative means of detection within the stomach would be to use stomach content DNA to determine prey diversity (Barnett et al. 2010, Carreon-Martinez et al. 2011). However, such methods are also subject to errors in the detectability of prey and as such should be used in combination with other methods (Hosseini et al. 2008).

The isotope mixing models are also known to be highly sensitive to discrimination factors (Bond & Diamond 2011). Yet the measurement of these factors can often be difficult for this kind of study. While extensive lab testing is often encouraged to determine these contributions (Gannes *et al.* 1997), many factors will influence the exact value of these factors within a given tissue type, including temperature (Barnes *et al.* 2007), feeding rate (Barnes *et al.* 2007), isotopic values of the prey (Caut *et al.* 2008, Caut *et al.* 2009), protein and fat content of the prey (McCutchan *et al.* 2003, Robbins *et al.* 2005) and approximate trophic position (Hussey *et al.*, 2014). In light of this wide range of uncertainty, I initially attempted to estimate a discrimination factor based on our observed stomach content information and isotope values of the prey. However, this

estimation sometimes produced unreasonable results likely due to the low sample sizes of stomachs for some species with a sometimes high percentage of empty stomachs. In these cases I used the measure provided by Post (2002) as an approximation with full knowledge that this estimate is likely a simplification of reality, yet robust enough to provide an interpretable outcome.

The number of potential prey sources were often quite high for many of the species analyzed. Previous work in this region identified over 100 different prey species within cod stomachs (Krumsick & Rose 2012). This number of potential prey sources is naturally beyond what the model can realistically handle. Group categories were created to account for minor contributions to the diets within stomach data in the present study and previously published studies. For species with particularly varied diets, this resulted in 14 prey categories as inputs into the model (Phillips *et al*. 2014). Although this situation is less than ideal, as over 7 prey categories are to be used with caution (Stock *et al.* 2018), I could not reasonably conclude that additional prey should be placed within the group categories given the prior information I have on this system. This assumption may lend itself to the results being slightly underdetermined, yet even so, given the entry of the priors, clear and interpretable results arose from the study.

Despite these uncertainties in the measures of the diet composition, the proportions represented by each prey item provide an indication of the relative importance of each prey item (Phillips et al. 2014). The isotope mixing models for more than 3 prey sources are based on probabilities of each prey item being selected and as such often have high variation as the resulting proportions are an average of 10,000 runs of the model.

Therefore, instead of focusing on determining the exactly proportions of each prey, I focused on determining key prey items for the food web as well as spatial variation in these trends. The use of stomach content information used as a prior helped to direct the measure of dietary proportions towards this end.

The Newfoundland and Labrador marine ecosystems are still in a state of recovery following overexploitation beginning decades ago (Lilly et al. 2008). Despite significant progress towards recovery, many groundfish populations have not yet reached the reference point for commercial exploitation (Pedersen et al. 2017, DFO 2018, Rose and Rowe 2018, Chapter 4), a process that can be limited by interspecific interactions (Fung et al. 2013). Through consideration of species interactions I have highlighted interactions between current and recovering fisheries to illustrate likely ecological and economic impacts of groundfish recoveries. As groundfish populations gradually approach a state where exploitation may resume in a sustainable manner, ecosystem and trophic dynamic considerations such as those presented should be considered in management decisions in order to facilitate ecosystem productivity and recovery. Such information gaps as trophodynamics and how they vary spatially are essentials inputs to ecosystem-based models that interact with other gaps such as essential fish habitat and population dynamics to help build an ecosystem framework of management (Slocomb 1993, Molina-Ureña & Ault 2007, Long et al. 2015).

Acknowledgements

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Supplementary Information

Table 3.S1 Definitions of species abbreviations

Species Abbreviation	Scientific Name	Common Name	Classification Category
AC	*Gadus morhua*	Atlantic Cod	Demersal Fish
AH	*Clupea harrengus harrengus*	Atlantic Herring	Pelagic Fish
AL	*Aspidophoroides monopterygius*	Alligatorfish	Demersal Fish
AM	Gammaridae	Gammarid Amphipod	Pelagic Invert
AP	*Hippoglossoides platessoides*	American Plaice	Demersal Fish
AR	*Boreogadus saida*	Arctic Cod	Pelagic Fish
AW	Chaetognatha	Arrow Worm	Pelagic Invert
BA	*Notolepis rissoi*	White Barracudina	Pelagic Fish
BG	*Benthosema glaciale*	Glacier Lanternfish	Pelagic Fish
BK	*Gorgonocephalus arcticus*	Basket Star	Benthic Invert
BP	-	Benthic Plants	Benthic Plant
BS	*Ophiopholus aculeata*	Brittle Star	Benthic Invert
BV	Bivalva	Bivalve	Benthic Invert
CA	*Mallotus villosus*	Capelin	Pelagic Fish
CE	*Lycodes vahlii*	Checkered Eelpout	Demersal Fish
CO	Copepoda	Copepod	Pelagic Invert
EU	Euphausiacea	Euphausiid	Pelagic Invert
FL	*Eumesogrammus pracisus*	Fourline Snakeblenny	Demersal Fish
GA	*Buccinum undatum*	Whelk	Benthic Invert
GH	*Reinhardtius hippoglossoides*	Greenland Halibut / Turbot	Pelagic Fish
HA	*Macruronus novaezelandiae*	Blue Hake	Demersal Fish
HO	Holothuroidea	Sea Cucumber	Benthic Invert
HS	*Artediellus atlanticus*	Hookear Sculpin	Demersal Fish
HY	Hyperiidea	Hyperiid Amphipod	Pelagic Invert
IS	Isopoda	Isopod	Benthic Invert
LH	*Urophycis chesteri*	Longfin Hake	Demersal Fish
MD	Mysidae	Mysid	Pelagic Invert
MG	*Nezumia bairdi*	Marlinspike Grenadier	Demersal Fish
MS	*Triglops murrayi*	Moustache Sculpin	Demersal Fish
MY	*Notoscopelus* sp.	Krøyer's Lanternfish	Pelagic Fish
NU	Nudibranchia	Nudibranch	Benthic Invert

OS	Ostracoda	Ostracod	Pelagic Invert
PO	Polychaeta	Polychaete	Benthic Invert
PP	-	Pelagic Algae	Pelagic Plant
PR	*Agonus decagonus*	Atlantic Poacher	Demersal Fish
PY	Pantopoda	Pycnogonid	Benthic Invert
RG	*Macrourus berglax*	Roughhead Grenadier	Demersal Fish
RF	*Sebastes* sp.	Redfish	Pelagic Fish
SA	Actiniaria	Sea Anemone	Benthic Invert
SB	*Lumpenus lumpretaeformis*	Snakeblenny	Demersal Fish
SC	*Chionocetes opilio*	Snow Crab	Benthic Invert
SF	Asteroidea	Sea Star	Benthic Invert
SH	*Pandalus* sp., *Sabinea sarsii*	Shrimp	Benthic Invert
SI	Sipuncula	Sipunculid	Benthic Invert
SQ	Decapodiformes	Squid	Pelagic Invert
SS	*Raja senta*	Smooth Skate	Demersal Fish
SU	*Strongylocentrotus droebachiensis*	Sea Urchin	Benthic Invert
TC	*Hyas* sp.	Toad Crab	Benthic Invert
TR	*Gaidropsarus ensis*	Three-beard Rockling	Demersal Fish
TS	*Raja radiata*	Thorny Skate	Demersal Fish
WF	*Glyptocephalus cynoglossus*	Witch Flounder	Demersal Fish

Table 3.S2 Definition of small, medium and large size categories for the most abundant nine fish species**.** Size category definitions were consistent across regions.

Species	Small size range (cm)	Medium size range (cm)	Large size range (cm)
American Plaice	7.0 – 22.6	22.7 – 38.3	38.4 – 54.0
Atlantic Cod	13.0 – 45.9	46.0 – 80.0	80.1 – 113.0
Atlantic Herring	27.1 – 30.9	31.0 – 34.7	34.8 – 38.5
Capelin	11.0 – 13.6	13.7 – 16.2	16.3 – 18.8
Checker Eelpout	8.0 – 20.9	21.0 – 33.9	34.0 – 47.0
Greenland Halibut	10.0 – 27.4	27.5 – 45.0	45.1 – 62.5
Lanternfish	12.9 – 14.5	14.6 – 15.6	15.7 – 17.4
Redfish	4.0 – 18.6	18.7 – 33.2	33.3 – 48.0
Thorny Skate	10.2 – 33.9	34.0 – 58.3	58.4 – 80.0

Table 3.S3 List of prey species/groups included in the isotope mixing model for each predatory fish species as determined from our stomach contents analyses and the presented studies from other researchers.

Species	Scientific Name	Prey Species/Groups	Diet Studies
Alligatorfish	*Aspidophoroides monopterygius*	Copepods, Euphausiids, Gammarids, Hyperiids, Isopods, Mysids, Polychaetes	Hutchings, 2002; Arbour *et al.*, 2010
American Plaice	*Hippoglossoides platessoides*	Bivalve, Brittlestar, Capelin, Copepod, Gammarid, Gastropod, Hookear Sculpin, Hyperiid, Mysid, Polychaete, Redfish, Shrimp, Snow Crab, Toad Crab	Powles, 1965; Pitt, 1973; Canalejo *et al.*, 1989; Keats, 1991; Zamarro, 1992; Martell and McClelland, 1994; Link *et al.*, 2002;
Arctic Cod	*Boreogadus saida*	Americna Plaice, Brittlestars, Copepods, Euphausiids, Gammarids, Hyperiids, Mysids, Redfish, Shrimp	Bohn and McElroy, 1976; Ajiad and Gjøsæter, 1990; Hobson and Welch, 1992; Hop *et al.*, 1997; Christiansen *et al.*, 2012; McNicholl *et al.*, 2016;
Atlantic Cod	*Gadus morhua*	Atlantic Herring, Capelin, Checkered Eelpout, Euphausiid, Hyperiid, Mysid, Polychaete, Redfish, Shrimp, Snow Crab, Benthic Invertebrates, Pelagic Invertebrates, Demersal Fish, Pelagic Fish.	Popova, 1962; Templeman, 1966; Turuk, 1968; Staneck, 1973; Staneck, 1975; Turuk, 1976; Minet and Perodou, 1978; Turuk and Postolaky, 1980; Lilly and Fleming, 1981; Bowering *et al*., 1983; Lilly and Rice, 1983; Lilly, 1984; Lilly and Osborne, 1984; Lilly, 1986; Methven and Piatt, 1989; Lilly, 1991; Gerasimova *et al.*, 1992; Lilly, 1994; Casas and Paz, 1996; Gerasimova and Kiseleva, 1998; DeBlois and

			Rose, 1996; Hanson and Chouinard, 2002; Link and Garrison, 2002; Krumsick and Rose, 2012; Pérez-Rodríguez and Saborido-Rey, 2012
Atlantic Herring	*Clupea harrengus harrengus*	Arrow Worms, Copepods, Euphausiids, Hyperiids, Mysids, Shrimp	Legaré and MacIellan, 1960; De Silva, 1973; Dalpadado *et al.*, 2000; Langøy *et al.*, 2012
Atlantic Hookear Sculpin	*Artediellus atlanticus*	Bivalves, Copepods, Euphausiids, Gammarids, Mysids, Polychaetes	Scott & Scott (1988)
Atlantic Poacher	*Agonus decagonus*	Bivalves, Brittlestars, Copepods, Gammarids, Mysids, Polychaetes	Scott & Scott (1988)
Capelin	*Mallotus villosus*	Arrow Worms, Copepods, Euphausiid, Gammarid, Gastropod, Hyperiid, Mysid, Polychaete, Shrimp	Vesin *et al.*, 1981; O'Driscoll *et al.*, 2001; Hedeholm *et al.*, 2012; Dalpadado and Mowbray, 2013
Checkered Eelpout	*Lycodes vahlii*	Bivalves, Brittlestars, Copepods, Gammarids, Hyperiids, Polychaetes, Shrimp	Albert, 1993
Fourline Snakeblenny	*Eumesogrammus pracisus*	Euphausiids, Gammarids, Mysids, Polychaetes, Shrimp	Hutchings, 2002
Glacier Lanternfish	*Benthosema glaciale*	Arrow Worms, Copepods,	Scott & Scott (1988)

		Euphausiids, Gammarids, Hyperiids, Mysids, Shrimp	
Greenland Halibut	*Reinhardtius hippoglossoides*	Atlantic Cod, Atlantic Herring, Capelin, Copepods, Checkered Eelpout, Gammarids, Hyperiid, Redfish, Shrimp, Squid, Benthic Invertebrates, Pelagic Invertebrates, Demersal Fish, Pelagic Fish	Chumakov and Podrazhanskaya, 1986; Bowering and Lilly, 1992; Rodríguez-Marín and Punzón, 1995; Orr and Bowering, 1997; Dawe *et al.*, 1998; Hovde *et al.*, 2002; Link *et al.*, 2002; Dwyer *et al.*, 2010
Krøyer Lanternfish	*Notoscopelus* sp.	Arrow Worm, Copepod, Euphausiids, Gammarids, Hyperiids, Mysid, Shrimp	Gjøsæter, 1981; Podrazhanskaya, 1993; García-Seoane *et al.*, 2013; Bernal *et al.*, 2015
Longfin Hake	*Urophycis chesteri*	Copepods, Euphausiids, Gammarids, Hyperiids, Lanternfish, Shrimp	Wenner, 1983; Methven and McKelvie, 1986; Pérez-Rodríguez *et al.*, 2011
Marlinspike	*Nezumia bairdi*	Bivalves, Copepods, Euphausiids, Gammarids, Hyperiids, Mysids, Polychaetes, Shrimp, Toad Crab	Savvatimsky, 1989; Pérez-Rodríguez *et al.*, 2011
Moustache Sculpin	*Triglops murrayi*	Copepods, Euphausiids, Gammarids, Mysids, Polychaetes, Shrimp, Toad Crab	Musick and Able, 1969; Atkinson and Percy, 1992
Redfish	*Sebastes* sp.	Brittlestars, Capelin, Copepods,	Steele, 1957; Lambert, 1960; Yanulov 1962; Canalejo *et*

		Euphausiids, Hyperiids, Lanternfishes, Mysids, Redfish, Shrimp, White Barracudina, Benthic Invertebrates, Pelagic Invertebrates, Demersal Fish, Pelagic Fish	*al.*, 1989; Albikovskaya and Gerasimova, 1993; Pedersen and Riget, 1993; González *et al.*, 2000; Savenkoff *et al.*, 2006; Pérez-Rodríguez and Saborido-Rey, 2012
Smooth Skate	*Raja senta*	Euphausiids, Gammarids, Mysids, Polychaetes, Redfish, Shrimp, Snow Crab, Toad Crab	McEachran *et al.*, 1976
Snakeblenny	*Lumpenus lumpretaeformis*	Bivalves, Copepods, Euphausiids, Gammarids, Mysids, Polychaetes, Sea Stars, Shrimp, Toad Crab	Demontigny *et al.*, 2012
Thorny Skate	*Raja radiata*	Capelin, Copepods, Euphausiids, Gammarids, Polychaetes, Redfish, Shrimp, Snakeblennies, Snow Crab, Squid, Benthic Invertebrates, Pelagic Invertebrates, Demersal Fish, Pelagic Fish	McEachran *et al.*, 1976; Templeman *et al.*, 1982; Pedersen, 1995; Garrison, 2000; Skjæraasen and Bergstad, 2000
Threebeard Rockling	*Gaidropsarus ensis*	Arrow Worms, Bivalves, Euphausiids, Gammarids,	Houston and Haedrich, 1986; Keats and Steele, 1990; Lampart-Kałużniacka and Heese, 2015

		Hyperiids, Mysids, Polychaetes, Shrimp	
White Barracudina	*Notolepis rissoi*	Copepods, Capelin, Euphausiids, Hyperiids, Mysids, Shrimp	Hutchings, 2002
Witch Flounder	*Glyptocephalus cynoglossus*	Bivalves, Euphausiids, Gammarids, Gastropods, Polychaetes, Mysids	Scott, 1976; Link *et al.*, 2002

Table 3.S4 Length-Weight Relationships of Representative Fish Species of Newfoundland and Labrador

Species	Length-Weight Relation	Reference
Alligatorfish	$W = 0.0029 * L^{3}$	Alpoim *et al.*, 2002
American Plaice	$W = 0.0036 * L^{3.305}$	Paz and Román, 1997
Arctic Cod	$W = 0.0119 * L^{2.76}$	Crawford and Jorgenson, 1996
Atlantic Cod	$W = 0.0081 * L^{3.044}$	Árnason *et al.*, 2009
Atlantic Herring	$W = 0.0097 * L^{2.96}$	Wigley *et al.* 2003
Atlantic Hookear Sculpin	$W = 0.02 * L^{2.85}$	Greenstreet *et al.*, 2012
Atlantic Poacher	$W = 0.0043 * L^{2.98}$	Alpoim *et al.*, 2002
Capelin	$W = 0.0042 * L^{3.11}$	Alpoim *et al.*, 2002
Checker Eelpout	$W = 0.0017 * L^{3.27}$	Alpoim *et al.*, 2002
Glacier Lanternfish	$W = 0.0054 * L^{3.08}$	Alpoim *et al.*, 2002
Greenland Halibut	$W = 0.005 * L^{3.1804}$	Román and Paz, 1997
Krøyer Lanternfish	$W = 0.0054 * L^{3.08}$	Alpoim *et al.*, 2002
Longfin Hake	$W = 0.0104 * L^{2.8226}$	Paz and Román, 1997
Marlin-spike	$W = 0.0254 * L^{2.89}$	Alpoim *et al.*, 2002
Moustache Sculpin	$W = 0.0032 * L^{3.46}$	Alpoim *et al.*, 2002
Redfish	$W = 0.0247 * L^{2.9364}$	Paz and Román, 1997
Roughhead Grenadier	$W = 0.1851 * L^{2.7542}$	Paz and Román, 1997
Smooth Skate	$W = 0.02 * L^{2.85}$	Paz and Román, 1997
Snakeblenny	$W = 0.0164 * L^{2.09}$	Alpoim *et al.*, 2002
Thorny Skate	$W = 0.0436 * L^{2.8611}$	Paz and Román, 1997
Three-beard Rockling	$W = 0.007 * L^{2.977}$	Alpoim *et al.*, 2002
White Barracudina	$W = 0.0003 * L^{3.58}$	Alpoim *et al.*, 2002
Witch Flounder	$W = 0.0008 * L^{3.497}$	Bowering and Stansbury, 1984

Table 3.S5 Fractionation coefficients and prey groups analyzed for the isotope mixing models of the remaining species. Percent IRI is presented in parentheses

Species	Fractionation Coefficient	Region	Prey species analyzed
Alligatorfish	4.2 / 0.1	HC	Gammarid (87.9%), Euphausiid (12.1%)
		BC	Copepod (72.4%), Polychaete (26.3%)
American Plaice	3.4 / 0.4	HC	Polychaete (65.8%), Brittlestar (17.8%), Toad Crab (6.3%), Hookear Sculpin (5.2%), Gammarid (2.3%), Shrimp (1.2%), Mysid (0.8%), Bivalve (0.3%), Copepod (0.3%)
		NDC	Toad Crab (67.8%), Polychaete (24.8%), Gammarid (7.4%)
		BC	Shrimp (44.9%), Bivalve (29.7%), Polychaete (18.3%), Gastropod (3.5%), Redfish (2.2%), Snow Crab (0.7%), Gammarid (0.6%)
Arctic Cod	3.4 / 0.5	HC	Copepod (43.8%), Shrimp (40.4%), Gammarid (15.8%)
		NDC	Copepod (85.0%), Hyperiid (12.9%), Shrimp (1.6%), Euphausiid (0.4%), Gammarid (0.1%)
		BC	Hyperiid (61.0%), Copepod (38.3%), Shrimp (0.4%), Gammarid (0.2%), Mysid (0.1%)
Atlantic Herring	3.3 / 0.3	HC	No food-containing stomachs.
		NDC	Hyperiid (94.2%), Euphausiid (4.1%), Copepod (1.5%), Shrimp (0.2%)
		BC	Hyperiid (100%)
Atlantic Poacher	3.9 / 0.4	HC	Gammarid (73.4%), Shrimp (15.1%), Polychaete (11.6%)
		BC	Gammarid (79.3%), Copepod (15.1%), Mysid (5.2%), Euphausiid (0.4%)
Capelin	3.4 / 0.4	HC	Copepod (75.0%), Mysid (14.8%), Hyperiid (9.5%), Euphausiid (0.4%), Polychaete (0.2%)
		NDC	Copepod (80.8%), Hyperiid (18.6%), Mysid (0.2%), Shrimp (0.2%), Euphausiid (0.1%), Gammarid (0.1%), Gastropod (0.1%)

		BC	Copepod (88.4%), Hyperiid (9.6%), Euphausiid (1.3%), Mysid (0.5%), Shrimp (0.2%)
Checkered Eelpout	3.4 / 0.4	HC	Polychaete (69.1%), Brittlestar (24.1%), Copepod (3.3%), Shrimp (2.4%), Bivalve (0.6%), Gammarid (0.6%)
		BC	Polychaete (79.7%), Copepod (7.1%), Hyperiid (7.0%), Gammarid (6.1%)
Fourline Snakeblenny	2.9 / -0.2	BC	Polychaete (100%)
Glacial Lanternfish	3.4 / 0.4	HC	Copepod (74.0%), Gammarid (13.0%), Shrimp (13.0%)
		NDC	Copepod (98.7%), Mysid (0.8%), Hyperiid (0.3%), Shrimp (0.3%)
Hookear Sculpin	3.0 / 0.9	HC	Bivalve (72.4%), Copepod (27.7%)
		NDC	Polychaete (66.7%), Copepod (16.7%), Gammarid (16.7%)
		BC	Copepod (63.0%), Gammarid (19.5%), Polychaete (9.5%), Mysid (4.9%), Euphausiid (3.1%)
Krøyer's Lanternfish	2.7 / 0.9	HC	Copepod (55.2%), Shrimp (23.1%), Hyperiid (18.7%), Euphausiid (1.7%), Mysid (1.3%), Gammarid (0.1%)
		NDC	Copepod (49.3%), Shrimp (36.2%), Hyperiid (13.8%), Mysid (0.8%)
		BC	Copepod (69.2%), Hyperiid (25.2%), Mysid (3.3%), Euphausiid (2.3%), Arrow Worm (0.1%)
Marlinspike	3.1 / 0.0	HC	Toad Crab (42.9%), Copepod (30.4%), Shrimp (17.0%), Hyperiid (9.8%)
		BC	Mysid (48.8%), Bivalve (29.0%), Polychaete (17.3%), Gammarid (3.5%), Shrimp (1.4%)
Moustache Sculpin	2.8 / 0.4	HC	Shrimp (65.5%), Polychaete (12.3%), Toad Crab (9.6%), Copepod (6.3%), Gammarid (6.3%)
		NDC	Hyperiid (70.0%), Gammarid (15.4%), Toad crab (8.4%), Polychaete (6.1%)
		BC	Shrimp (32.5%), Mysid (22.5%), Copepod (22.5%), Gammarid (22.5%)

Roughhead Grenadier	3.0 / 0.4	HC	Copepod (46.2%), Gammarid (23.7%), Polychaete (21.4%), Shrimp (4.9%), Brittle Star (1.3%), Snow Crab (0.9%), Euphausiid (0.8%), Mysid (0.6%)
Smooth Skate	1.4 / 0.5	HC	Shrimp (49.5%), Euphausiid (43.1%), Polychaete (4.0%), Gammarid (3.3%)
		BC	Shrimp (72.1%), Toad Crab (27.9%)
Snakeblenny	4.1 / 0.4	HC	No prey-containing stomachs
		BC	Toad Crab (100%)
Thorny Skate	2.5 / 0.2	HC	Shrimp (75.2%), Polychaete (10.1%), Snow Crab (9.0%), Euphausiid (1.3%), Gammarid (1.3%), Benthic Invertebrates (1.3%), Copepod (0.9%), Squid (0.5%), Capelin (0.1%), Demersal Fish (0.1%), Pelagic Invertebrates (0.1%)
		NDC	No prey-containing stomachs
		BC	Shrimp (29.0%), Euphausiid (27.2%), Polychaete (11.2%), Capelin (7.0%), Snow Crab (7.0%), Pelagic Invertebrate (6.3%), Gammarid (5.3%), Benthic Invertebrates (2.7%), Snakeblenny (1.7%), Demersal Fish (1.4%), Copepod (1.0%), Redfish (0.2%), Squid (0.1%)
Threebeard Rockling	3.4 / 0.5	HC	No prey-containing stomachs
		BC	Shrimp (72.9%), Hyperiid (8.4%), Polychaete (7.3%), Mysid (4.5%), Euphausiid (3.4%), Gammarid (3.4%)
White Barracudina	3.4 / 0.4	HC	Shrimp (71.8%), Copepod (19.8%), Euphausiid (4.9%), Capelin (1.9%), Hyperiid (1.2%), Gammarid (0.2%), Mysid (0.2%)
		NDC	Shrimp (61.8%), Copepod (34.3%), Hyperiid (1.8%), Mysid (1.6%), Euphausiid (0.4%)
		BC	Copepod (80.1%), Shrimp (18.6%), Euphausiid (1.1%), Hyperiid (0.3%)
Witch Flounder	3.4 / -0.1	HC	No prey-containing stomachs
		NDC	

	BC	Polychaete (79.3%), Gammarid (13.2%), Euphausiid (5.2%), Bivalve (1.2%), Mysid (1.1%)

Table 3.S6 Isotope sample sizes by region and size category with food-containing stomach sample sizes.

	Region	Small	Medium	Large	Stomach Samples
American Plaice	HC	4	10	7	26
	NDC	5	12	4	2
	BC	7	7	7	13
Atlantic Cod	HC	7	8	6	8
	NDC	7	9	4	15
	BC	7	7	7	16
Atlantic Herring	HC	0	2	0	0
	NDC	4	3	1	18
	BC	1	3	5	4
Capelin	HC	0	3	5	6
	NDC	0	5	4	31
	BC	3	3	3	14
Checker Eelpout	HC	3	3	3	9
	NDC	0	0	0	0
	BC	3	4	3	10
Greenland Halibut	HC	8	7	6	19
	NDC	8	7	1	15
	BC	5	9	7	15
Lanternfish	HC	3	3	4	30
	NDC	3	4	2	8
	BC	3	3	3	12
Redfish	HC	5	8	8	16
	NDC	7	7	7	14
	BC	7	7	7	7
Thorny Skate	HC	8	9	1	12
	NDC	0	3	0	0
	BC	7	11	3	26

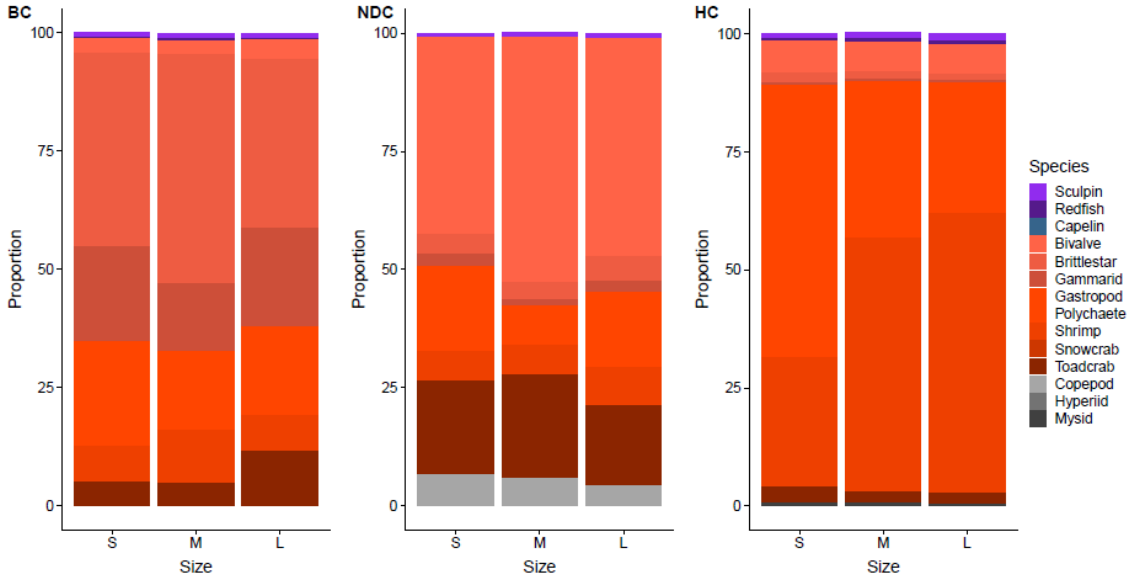

Fig. 3.S1 American Plaice diet composition as determined from isotope mixing models divided by size category and region.

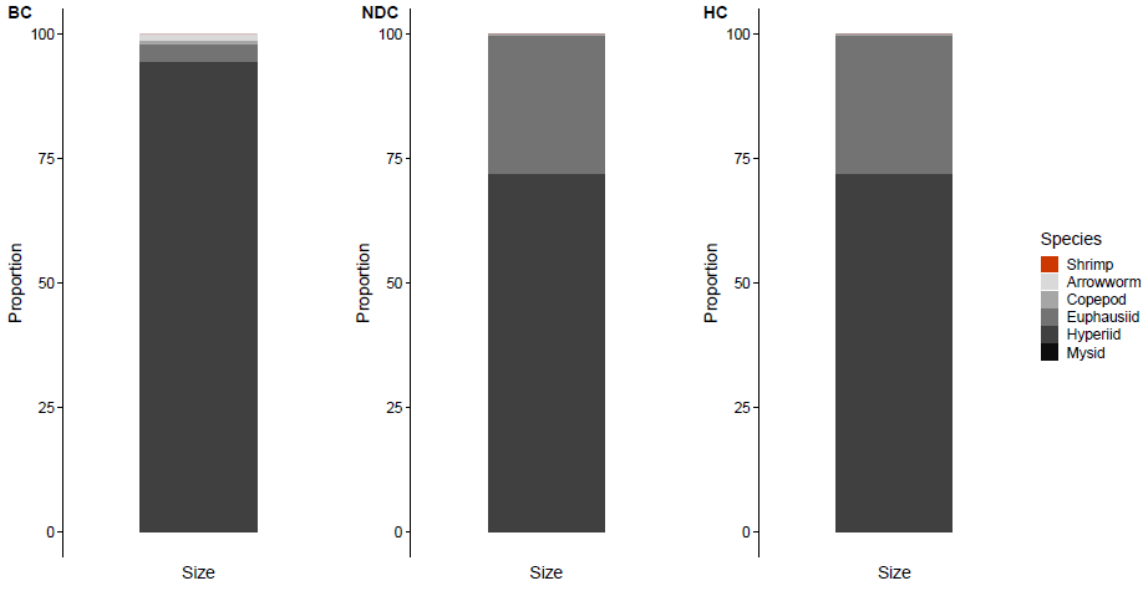

Fig. 3.S2 Atlantic Herring diet composition as determined from isotope mixing models divided by size category and region.

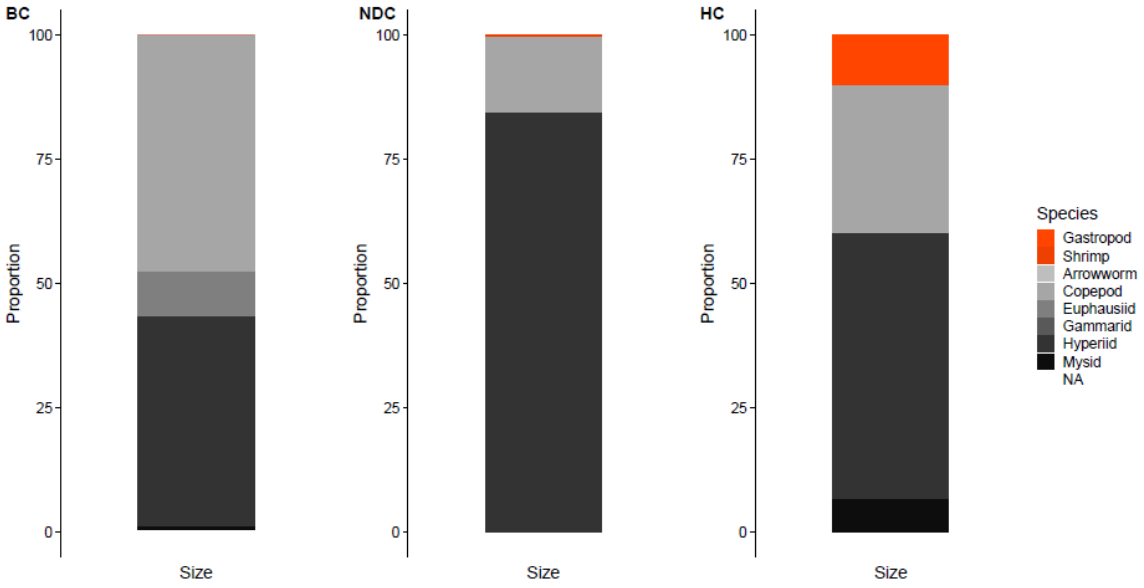

Fig. 3.S3 Capelin diet composition as determined from isotope mixing models divided by size category and region.

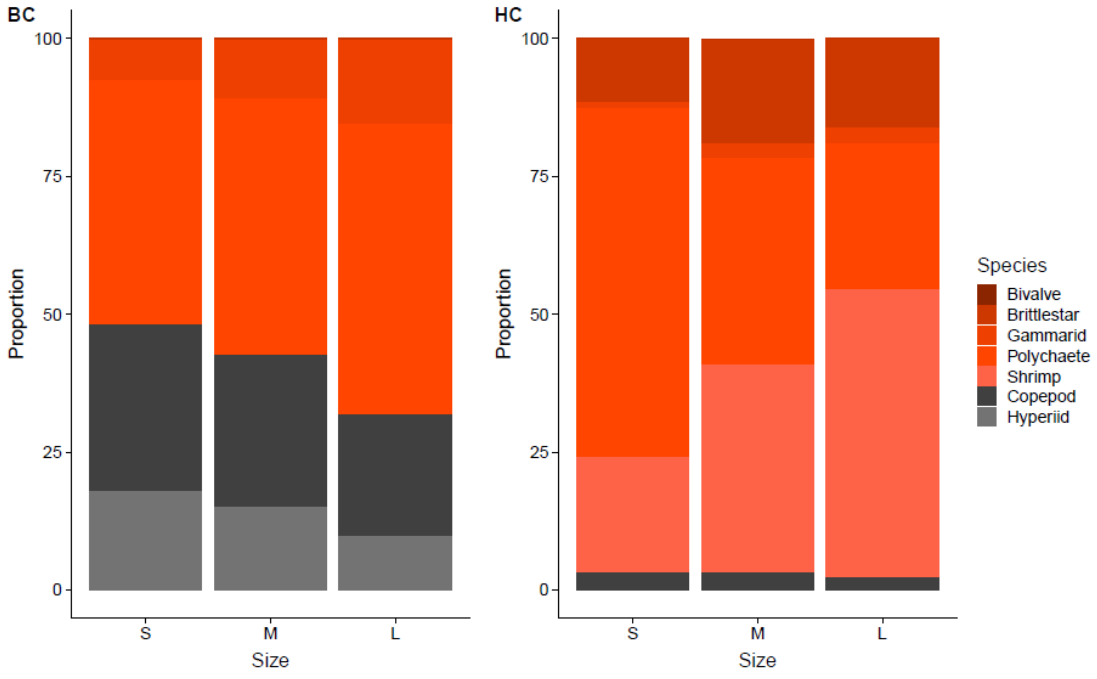

Fig. 3.S4 Eelpout diet composition as determined from isotope mixing models divided by size category and region.

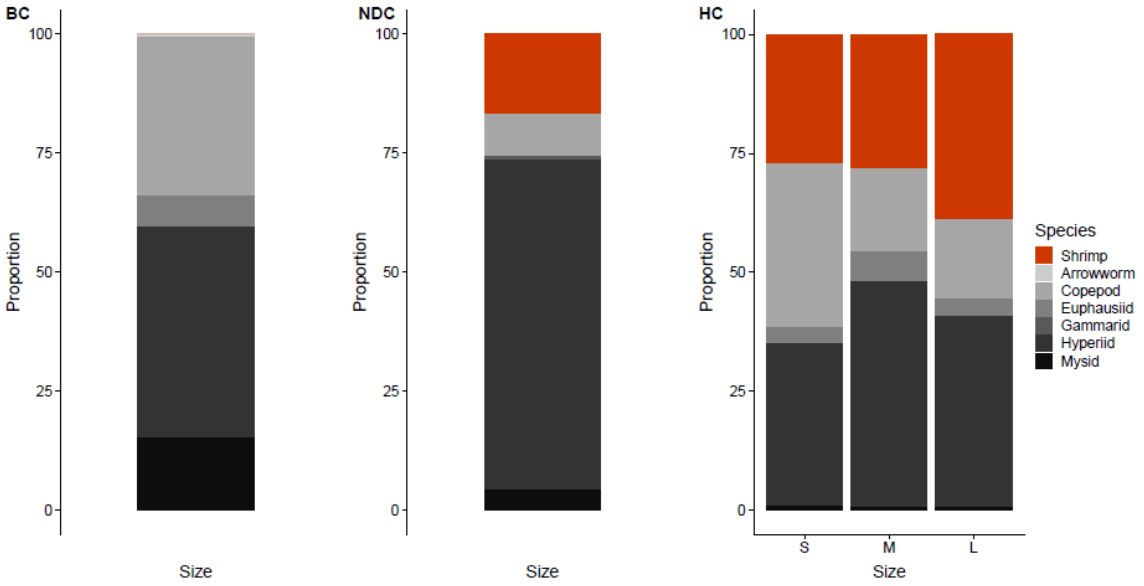

Fig 3.S5 Lanternfish diet composition as determined from isotope mixing models divided by size category and region.

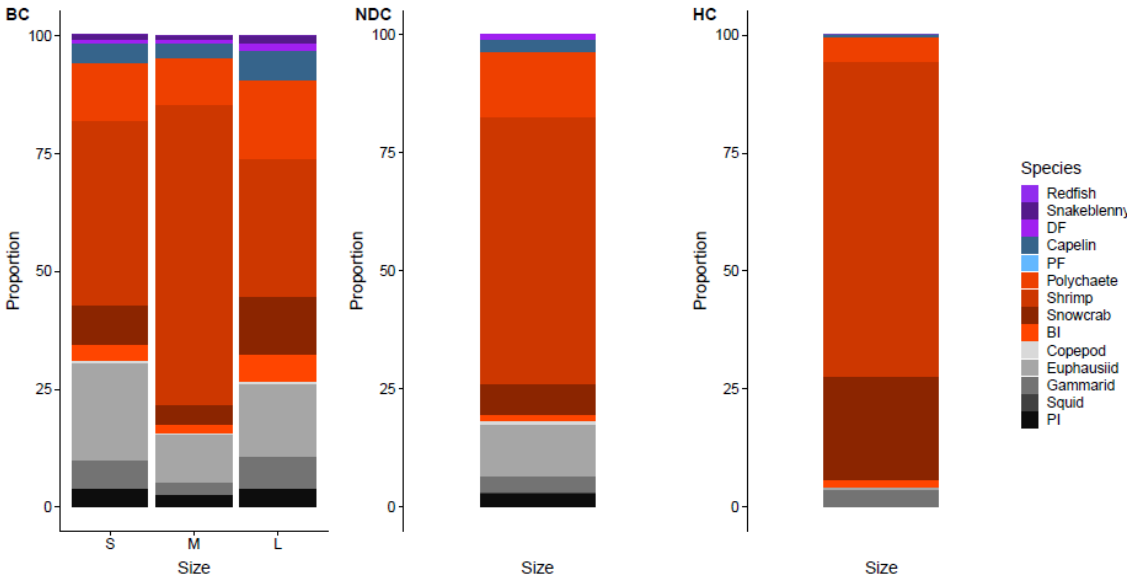

Fig 3.S6 Thorny Skate diet composition as determined from isotope mixing models divided by size category and region. Functional group categories are designated by two letter abbreviations: PI for pelagic invertebrates, BI for benthic invertebrates, PF for pelagic fish, DF for demersal fish.

Chapter 4: Community size spectra provide indicators within recovering fisheries ecosystems on the Newfoundland and Labrador shelf.

Abstract

Species- and size-selective overexploitation often have ecosystem-wide impacts that are evident in community size-spectra. To both derive potential ecosystem targets for community rebuilding and assess contemporary indicators relative to these targets, I constructed theoretical size-spectra to predict pristine biomass densities using a combination of species- and size-specific nitrogen stable isotope signatures and a range of trophic efficiencies and primary productivity estimates within and among three sub-regions of the Newfoundland and Labrador shelf. Theoretical size-spectra were compared to empirically-derived size spectra using trawl survey data. The descending slopes of the empirically determined size spectra were between 1.25 and 2.42 times steeper than the theoretical slopes. The percentage of the theoretical distribution represented by the empirical size structure ranged between 1.1 and 29.4%, with the closest and furthest estimates associated with smallest and largest sized fishes, respectively, and strongly influenced by estimates of trophic efficiency and primary productivity. Regional variation was also observed with southern regions reaching 1.3 – 32.3% of the theoretical biomass density and the northernmost region only 0 – 8.3%. Importantly, the descending slopes varied depending on fish size, with biomass density of larger sizes decreasing faster than smaller sizes. Variations among sub-regions and fish guilds Ire also observed. These analyses provide a means to derive potential ecosystem targets and indicators through which recovery of fish communities can be monitored and assessed.

Introduction

Both biomass densities and the abundances of organisms have been observed to decrease with increasing body size (White et al. 2007), a relationship that is the foundation for size spectra modeling (Sheldon et al. 1972). These models treat organisms solely on the basis of size, thereby concealing taxonomic identity (Petchey & Belgrano 2010), and have been used extensively to model size-structured marine ecosystems (Blanchard et al. 2017). Since growth is dependent on food intake, size-structured models are considered a subset of physiologically structured models (De Roos & Persson 2001). The expanding field of size-structure models helps explain community organization (Shin et al. 2005, Hartvig et al. 2011, Blanchard et al. 2017) and community responses to anthropogenic influences, including climate change, species invasions, and exploitation (Jennings & Blanchard 2004, Andersen & Rice 2010, Petchey & Belgrano 2010, Woodward et al 2010, Engelhard et al. 2014, Jacobsen et al. 2014). As management of marine fisheries moves towards community and ecosystem approaches (Mangel & Levin 2005), it is necessary to evaluate community and ecosystem indicators relative to new or established conservation targets (Shin et al. 2005, Jennings & Dulvy 2005).

Fishing pressure and climate change represent two of the greatest anthropogenic pressures facing marine communities (Jackson et al. 2001, Tremblay-Boyer et al. 2011). Larger individuals and species are often selectively captured by commercial fishing, reducing predation pressure and leaving remaining individuals to exhibit increases in biomass to fill the opened ecological niches (Anderson & Rice 2010). This can result in observed decreases in the species-specific maximum length (Hixon et al. 2014), mean

length in a community (Fisher et al. 2010; Shin et al. 2005), and a steeper descending slope of community size spectra (Pimm & Hyman 1987, Jennings & Blanchard 2004, Daan et al. 2005, Shin et al. 2010). Quantifying such changes within ecosystems having a long history of exploitation from a size-spectrum perspective requires both quantifying the current state and identifying a baseline reference state (Jennings & Blanchard 2004).

In the 1980s and early 1990s, demersal fisheries in the Newfoundland and Labrador region experienced high levels of exploitation during poor environmental conditions leading to stock collapses and subsequent declaration of fisheries moratoria on Atlantic cod (*Gadus morhua*), and other co-occurring species (Lilly et al. 2008). The loss of this top predator was associated with ecosystem-wide changes (Lilly et al. 2000, Rice 2002, Frank et al. 2006, Pedersen et al. 2017), including the size structure of shelf communities (Haedrich & Barnes 1997, Fisher et al. 2010). This marine ecosystem is presently recovering from overexploitation (Pedersen et al. 2017, DFO 2018), a process that from a size-structure perspective may take decades (Fung et al. 2013). The earliest recorded accounts of exploitation of this ecosystem date to the late fifteenth century (Cell 1982, Rose 2007). Therefore, establishing a baseline to assess contemporary recovery based on historical data is challenging and has been attempted only for Atlantic cod populations in these systems (Myers et al. 2001, Rose 2004). Here I conduct analyses that provide complimentary community-level baselines and contemporary indicators of ecosystem recovery focusing on a broad base of size-classes and species.

Using methods first proposed by Jennings & Blanchard (2004), I compiled data from three sub-regions within the Newfoundland and Labrador Shelf ecosystem to quantify the

current status of the marine fish communities in the context of ecosystem 'recovery' and its variation among sub-regions and body size classes. Jennings & Blanchard (2004) integrated predator-prey mass ratio (PPMR) data, estimates of primary productivity, and a range of ecologically reasonable trophic efficiency estimates, defined as the proportion of consumed energy that consumers convert to biomass in one trophic level, to provide theoretically expected biomass densities across a wide range of fish sizes within North Sea fish communities. However, Jennings & Blanchard (2004) also noted that it was uncertain whether the cessation of fishing would allow recovery to an unexploited community size structure and that question was beyond their North Sea analyses. Therefore, I sought to quantify the extent of community reversion towards a theoretical unexploited state over 25 years after the initial groundfish fisheries moratoria were established in Newfoundland. By similarly deriving theoretical biomass densities for the Newfoundland and Labrador Shelf communities, our study addresses the questions: How far is the current biomass of fish communities from a theoretical unexploited biomass? Furthermore, do empirical community-level signatures of prior overexploitation remain evident over two decades later? Separate analyses were conducted among the three regions and within three size categories of fishes to further partition the community-wide impacts of past exploitation. The three sub-regions are known to differ in prey species richness and trophic overlap (Chapter 2).

MATERIALS & METHODS

Study Area

The study was conducted as part of acoustic-trawl surveys conducted by the Center for Fisheries Ecosystems Research (CFER) aboard the RV Celtic Explorer in May 2013 and 2015 on the offshore shelves from southern Labrador and eastern Newfoundland, in Northwest Atlantic Fishery Organization (NAFO) subdivisions 2J, 3K, and 3L (Rose & Rowe 2018, Fig 4.1). Combined these subdivisions represent the management unit for the 'Northern cod' stock of Atlantic cod (Templeman 1979, Rose et al. 2000, Smedbol & Wroblewski 2002). Set locations were chosen based on information obtained from acoustic signals for cod and other species. Sets in the absence of cod acoustic signals were also undertaken to compliment these targeted sets. Sets averaged 11-13 fish species per set (Chapter 2) with no significant differences in the number of fish species per set between cod targeted sets and other sets (one-way ANOVA: HC $p = 0.760$, NDC $p = 0.760$, BC $p = 0.371$). Three major trenches or corridors within these regions had previously been identified as important onshore-offshore cod migration pathways: Hawke Channel, Notre Dame Channel, and the Bonavista Corridor (Rose 1993). Given their potential importance, these trenches served as the focal regions for sampling. The following analyses were therefore conducted for each region separately then pooled for the entire region in order to both assess spatial variation in size spectra and to define trends for the entire region. Data for the fish species relative biomass composition and numbers were collected in May 2013 using a Campelen 1800 trawl (Walsh & McCallum

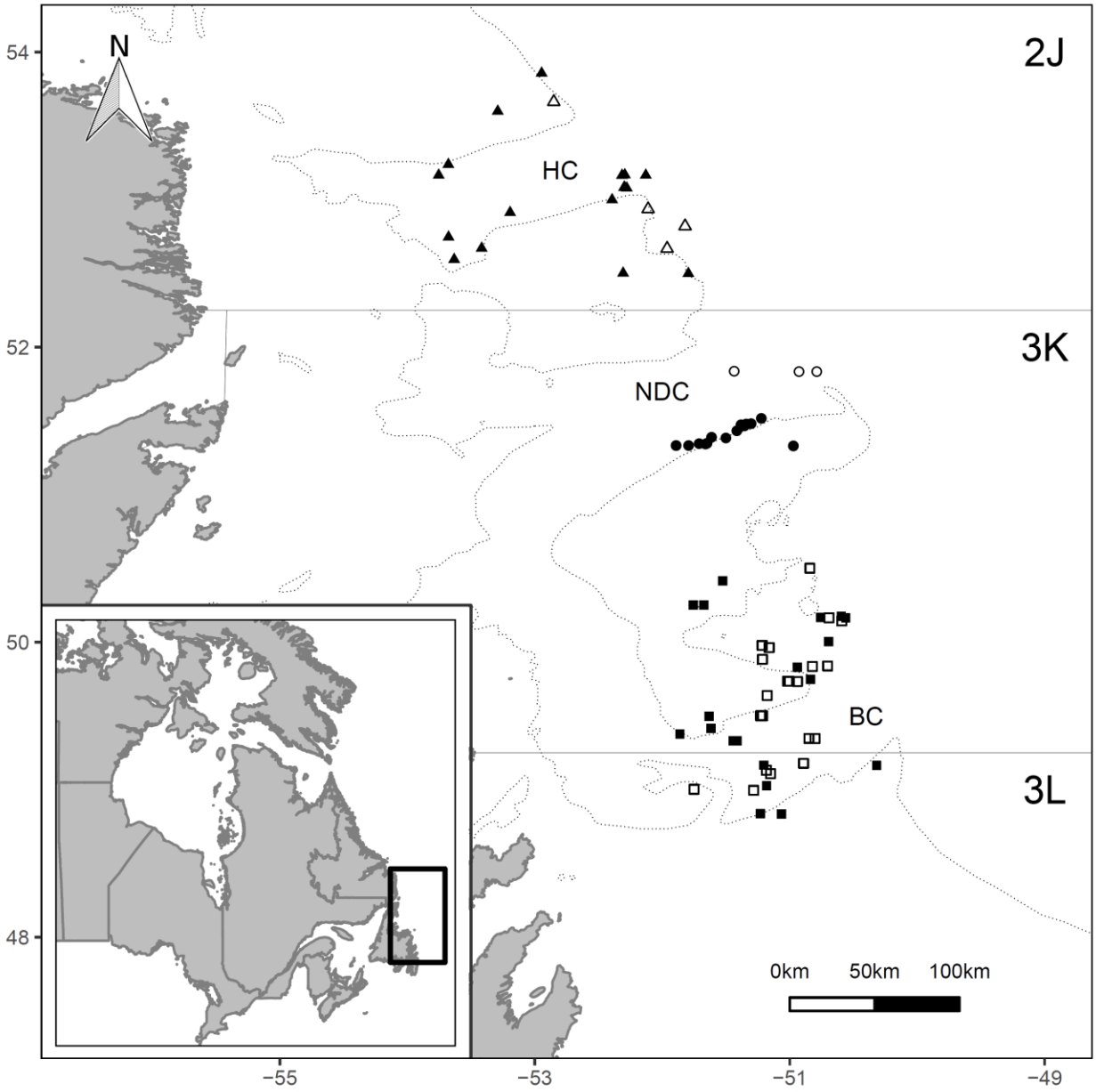

Fig. 4.1 Map of Newfoundland and southern Labrador with sampling locations**.** The sampling locations are indicated for the 2013 (open symbols) and 2015 (closed symbols) locations within the Hawke Channel (HC, triangles), Notre Dame Channel (NDC, circles), and Bonavista Corridor (BC, squares). The inset map outlines the study domain in eastern Canada. The relevant NAFO subdivisions 2J, 3K, and 3L boundaries are also indicated. Dashed lines represent 300 m depth contours. The bathymetry map is reproduced from GEBCO world map 2014 (www.gebco.net) and NAFO subdivisions reproduced from NAFO (www.nafo.int).

1997). Samples for nitrogen isotope analysis were collected during May, 2015, utilizing a combination of Campelen 1800, and mid-water trawl (Table 4.S1). Though sets ranged in duration from 5 to 20 minutes as determined by the chief scientist, all tows were conducted at a constant speed of 3.5 knots. The area sampled was therefore calculated from this distance towed in combination data provided by Marport sensors attached to the trawl to determine mouth width.

Sample collection and preparation

During both years, all fish caught were sorted by species and standard lengths were recorded. The total biomass of each species was also assessed. In cases where a species was particularly abundant, subsampling was initiated involving 100 randomly sampled individuals. In 2015 tissue samples were taken from all fish species with equal representation from the observed size ranges for each species. From most fish, a transverse sample of dorsal muscle tissue directly posterior to the head was collected at-sea, placed in a 1.5 ml centrifuge vial and frozen at -20 ºC. Frozen stomach samples were also collected from these fish at-sea. Remaining fish with small, difficult to sample stomachs were individually labelled and bagged, frozen whole at-sea and later dissected in the laboratory for their muscle tissue and stomachs.

Muscle tissue samples were oven dried at 75°C for 48 hours and homogenized using an amalgamator. The dry, homogenized samples were shipped to the Cornell University Stable Isotope Laboratory (Ithaca, New York, USA) for weighing and analysis. Approximately 1 mg of the powdered sample was placed into 7x7 mm tin capsules.

These samples were flash combusted using a Carlo-Erba NC2500 elemental analyzer coupled on-line to a Finnigan MAT Delta Plus mass spectrometer for analyses of the nitrogen gases.

Empirical size spectra

Analyses for this study were conducted in R version 3.5.3 (R Core Team 2019). A visual representation of the analytical methods and inputs is presented in Fig 4.S1. Fish length data from the 2013 samples were converted to mass of individual fish mostly through species-specific length-weight relationships (Table 4.S2). For the 2248 measured weights, there was ~1:1 correspondence with species-specific length-weight relationships (Fig 4.S2). However, when the weight of an individual fish was recorded, empirical weights (g) were used. Species-specific biomasses were also adjusted by dividing by the catchability, assumed to be 0.25 (Jennings et al. 2002), unless published species- and size-specific estimates were available (available for 53% of species sampled; Table 4.S2). To generate the size spectra, I followed recommendations provided by Edwards et al. (2017), although the prescribed Maximum Likelihood Estimate approach was found to depart from the empirical data (Fig 4.S3). Fish masses were binned into $\log_2$ mass categories (M). The total observed biomass at M was converted to density (g/m^2) by dividing by the swept area of the trawl (distance trawled x wing spread). Data collected from each set were treated in this manner and the mean binned biomass density obtained among sets was used to account for varying set durations. These biomass densities were divided by the width of the $\log_2$ mass category to create a mean binned normalized

biomass density (B). Size spectra were then plotted as $\log_{10}$B as a function of $\log_{10}$M, starting at 64 g, to determine the scaling coefficient between the two variables. Separate analyses were conducted across each sub-region as well as pooled including all three sub-regions.

I further assessed variation in size-spectra slopes among size categories and fish guilds. As per Daan et al. (2005), empirical size spectra were analyzed as described above but for three separate size groups: small: M < 4 kg, medium: M 4 - 8 kg, and large: M > 8 kg. Five separate size spectra were created for guilds of fish (flatfishes, pelagics, gadoids, elasmobranchs, and demersal mesopredators; Table 4.1) to assess whether the size spectra slopes observed in guilds differed systematically from the community slope. Guild-specific size spectra were calculated within the size categories identified above, but pooled across regions.

Quantification of unexploited size spectra

The nitrogen ratios from analyzed fish tissue samples were expressed in delta (δ) notation, representing the parts per thousand deviation from the standard material (i.e. atmospheric nitrogen). The calculation for delta is as follows:

$$\delta^{15}N = \left(\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right) \times 1000 \quad (1)$$

$$R = {}^{15}N/{}^{14}N \quad (2)$$

The $\delta^{15}N$ estimates were then converted to trophic level estimates using the equation:

$$TL = \left(\frac{\left(\delta^{15}N - \delta^{15}N_{ref}\right)}{3.4}\right) + 2 \quad (3)$$

Table 4.1 Fish species categorized within five guilds with percentage of sampled biomass during the 2013 survey presented next to each species name. Numbers of individuals in each size category for each guild are also displayed.

Guild	Species included (Percent of subgroup biomass)	Size	Number
Flatfishes	Greenland Halibut (*Reinhardtius hippoglossoides*, 81.7%), American Plaice (*Hippoglossoides platessoides*, 14.4%), Witch Flounder (*Glyptocephalus cynoglossus*, 4.0%).	< 4 kg	1512
		4 – 8 kg	0
		> 8 kg	0
Pelagics	White Barracudina (*Notolepis rissoi*, 36.0%), Myctophiid (*Notoscopelus* sp. and *Benthosema glaciale*, 34.5%), Atlantic Herring (*Clupea harrengus harrengus*, 18.2%), Capelin (*Mallotus villosus*, 9.2%), Stout Sawpalate (*Serrivomer beani*, 1.8%), Viperfish (*Chauliodus sloani*, 0.1%), Atlantic Argentine (*Argentina silus*, < 0.1%), Anglerfish (*Oneirodes macrosteus*,< 0.1%), Lightless Loosejaw (*Malacosteus niger*, < 0.1%).	< 4 kg	478
		4 – 8 kg	0
		> 8 kg	0
Gadoids	Atlantic Cod (*Gadus morhua*, 99.9%), White Hake (*Urophycis tenuis*, 0.1%), Arctic Cod (*Boreogadus saida*, < 0.1%), Longfin Hake (*Urophycis chesteri*, < 0.1%), Threebeard Rockling (*Gaidropsarus ensis*, < 0.1%).	< 4 kg	2728
		4 – 8 kg	393
		> 8 kg	28
Elasmobranchs	Thorny Skate (*Raja radiata*, 99.9%), Smooth Skate (*Raja senta*, 0.1%).	< 4 kg	91
		4 – 8 kg	12
		> 8 kg	2
Demersal mesopredators	Redfish (*Sebastes* sp., 91.1%), Checker Eelpout (*Lycodes vahlii*, 3.2%), Atlantic Wolffish (*Anarhichas lupus*, 2.0%), Atlantic Hookear Sculpin (*Artediellus atlanticus*, 0.8%), Marlin-spike (*Nezumia bairdi*, 0.7%), Nothern Wolffish (*Anarhichas denticulatus*, 0.6%), Atlantic Lumpfish (*Cyclopterus lumpus*, 0.3%), Moustache Sculpin (*Triglops murrayi*, 0.2%), Bigeye Sculpin (*Triglops nybelini*, 0.1%), Spotted Wolffish (*Anarhichas minor*, 0.1%), Alligatorfish (*Aspidophoroides monopterygius*, < 0.1%), Atlantic Poacher (*Agonus decagonus*, < 0.1%), Daubed Shanny (*Lumpenus maculatus*, < 0.1%), Fourline Snakeblenny (*Eumesogrammus pracisus*, < 0.1%) Sea Tadpole (*Careproctus reinhardti*, < 0.1%), Shorthorn Sculpin (*Myoxocephalus scorpius*, < 0.1%), Snakeblenny (*Lumpenus lumpretaeformis*, < 0.1%), Wolf Eelpout (*Lycenchelys verrilli*, < 0.1%), Wrymouth (*Cryptacanthodes maculatus*, < 0.1%).	< 4 kg	2292
		4 – 8 kg	2
		> 8 kg	0

The previous equation assumes a fractionation coefficient of 3.4 (Post 2002). The $\delta^{15}N_{ref}$ represents the nitrogen signature of a species close to the base of the food chain, in our case the herbivorous copepod *Calanus finmarchicus* (Dakin 1908, Marshall & Orr 1955, Nejstgaard et al. 1997). A linear relationship was determined between the trophic level and the logged mass of the fish (M). The predator-prey body size ratio was determined from this linear relation by the relation $PPMR = 10^{\frac{1}{b}}$ where b is the slope of the regression line fitted between the trophic level and logged mass (Jennings & Blanchard 2004).

The intercept of the theoretical unexploited size spectrum was estimated using primary productivity estimates obtained from the literature (Table 4.S3). A value of 336 $g\ C\ m^{-2}y^{-1}$ (midway between extremes among estimates; Table 4.S3) was used to define the theoretical size structure with error bars derived from the highest (540 $g\ C\ m^{-2}y^{-1}$) and lowest (132 $g\ C\ m^{-2}y^{-1}$) and lowest published estimates. The primary production does not influence the magnitude of the descending slope but rather the intercept of the theoretical distribution. Primary productivity estimates were converted to annual wet weight (grams) produced per square meter following Greenstreet *et al.* (1997). The relationship between trophic level (TL) and $\log_2$ mass category (M) was derived from the PPMR relationship determined previously where TL = a + b log M. The production at trophic level that the ecosystem could sustain given this primary production was calculated as $P_{TL} = PP * TE^{(TL-1)}$, analyzed for three values of trophic efficiency (TE = 0.1, 0.125, and 0.15), consistent with marine ecosystems in other parts of the world (Ware 2000, Jennings & Blanchard 2004). The production (P) at a given trophic level

was converted to biomass (B) at trophic level through the relationship $P: B = 2\,M^{-0.25}$ (Banse & Mosher 1980). In order to compare to the empirical size distribution, the theoretical distribution was normalized by dividing the biomass estimates by the width of the same $\log_2$ size categories. The descending slope of the theoretical size distribution was calculated from the linear relationship of the normalized theoretical biomass density (B) and $\log_2$ body mass category (M). These analyses were conducted at a community level and for each of the three sub-regions.

Statistical analyses

Differences in the slope of both the empirical and theoretical biomass density (B) against body mass (M) between regions was determined using an ANCOVA with body mass and region as explanatory variables. To test for linearity between the empirical biomass density and body mass, Ramsey's RESET test for functional form was implemented (Ramsey 1969). Differences in the slope of the regression between trophic level and logged body mass and region was also assessed with an ANCOVA. Furthermore, an ANCOVA was used to determine whether the slope between size categories differed in the regression of trophic level and logged body mass. The mean trophic level for fish within the same size range was compared among regions using an ANCOVA predicting trophic level from region and fish mass.

Results

Species composition

A total of 38 fish species were recorded during the 2013 survey (Table 4.1). The Hawke Channel was dominated by redfish (50% by biomass; 50% by numbers) and Atlantic cod (29%; 8%). Similarly, the Notre Dame Channel was dominated by Atlantic cod (60%; 34%) and redfish (28%; 41%), while the Bonavista Corridor biomass was nearly exclusively composed of Atlantic cod (82%; 29%) with redfish (7%; 37%) making a minor contribution. For the entire study area, the contributions of cod was 78% by biomass and 31% by numbers and redfish was 15% and 36%, respectively, with other notable species being Greenland halibut (4%, 7%) and American plaice (1%, 9%). In both 2013 and 2015, the Bonavista Corridor was more extensively surveyed resulting in larger sample sizes (Table 4.1, Table 4.S4). In 2013 there were no fish larger than 8 kg collected in the Hawke Channel or the Notre Dame Channel region, although one was caught in the Hawke Channel in 2015. The two species whose observed body sizes exceed 8 kg were Atlantic cod and thorny skate.

Body Size and Trophic Level Relation

The derived trophic level at which fish fed was found to increase nearly linearly with log body mass ($p < 0.001$; Fig 4.2). For the entire area, the increase in trophic level with size was described by the linear function $TL = 0.37 \log (M) + 3.07$. The slope of this relationship represented a species-averaged PPMR of 521:1. When divided by regions, the PPMR was 64:1 within the Notre Dame Channel, lower than either the Bonavista

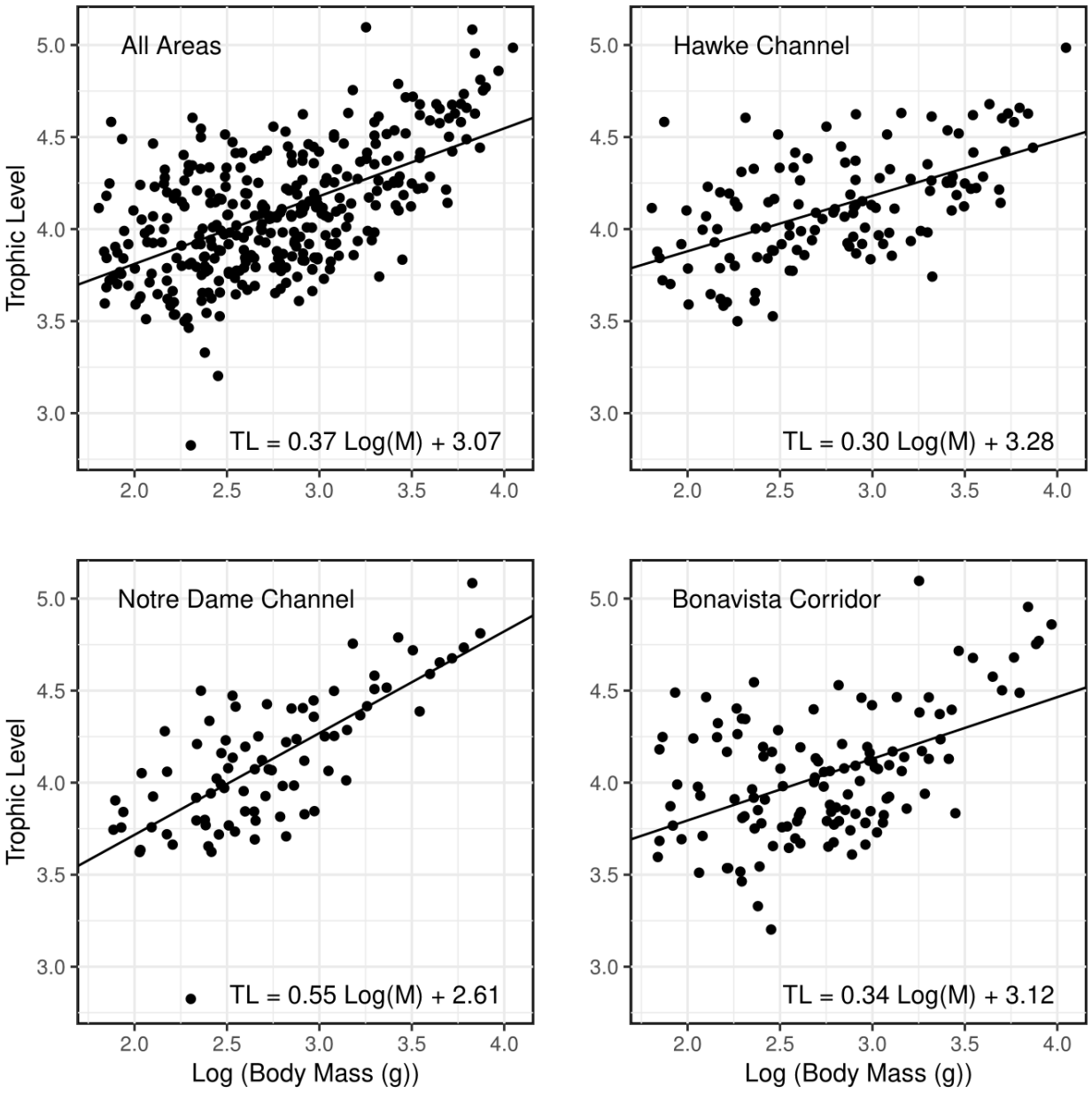

Fig. 4.2 Regression analysis of the increase in trophic level with logged body mass to determine predator-prey mass ratios (PPMR) for each region.

Corridor (966:1) or the Hawke Channel (2110:1) ($p = 0.003$), indicating that fish in the Hawke channel appear to be feeding on smaller prey. There is insufficient evidence to say that the slope of the linear regression between trophic level and logged body mass varied among small, medium, and large body size categories ($p = 0.27$).

Theoretical Size Structure

The slopes of the theoretical size spectra ranged from -0.43 to -0.74 with lower trophic efficiencies yielding steeper slopes (Fig 4.3, Table 4.2). The descending slopes of the Hawke

Channel and the Bonavista Corridor were comparable while the Notre Dame Channel showed a steeper decline in biomass with increasing body size due to lower PPMR ($p < 0.001$; Table 4.2).

Empirical size spectra

As expected, the biomass of fishes declined with increasing body mass ($p < 0.001$; Fig 4.3). In the empirical community, and assuming a linear relationship, biomass for the entire pooled regions was observed to scale as $M^{-0.69}$ (Table 4.3). Slopes within sub-regions (pooled sizes) ranged from -0.69 to -1.04, though these slopes did not differ significantly ($p = 0.603$; Table 4.3). In most cases the relationships were not linear (testing for non-linearity yielded $p = 0.01$ for Bonavista Corridor and $p = 0.04$ for Notre Dame Channel) as residuals were not randomly distributed; Hawke Channel was the

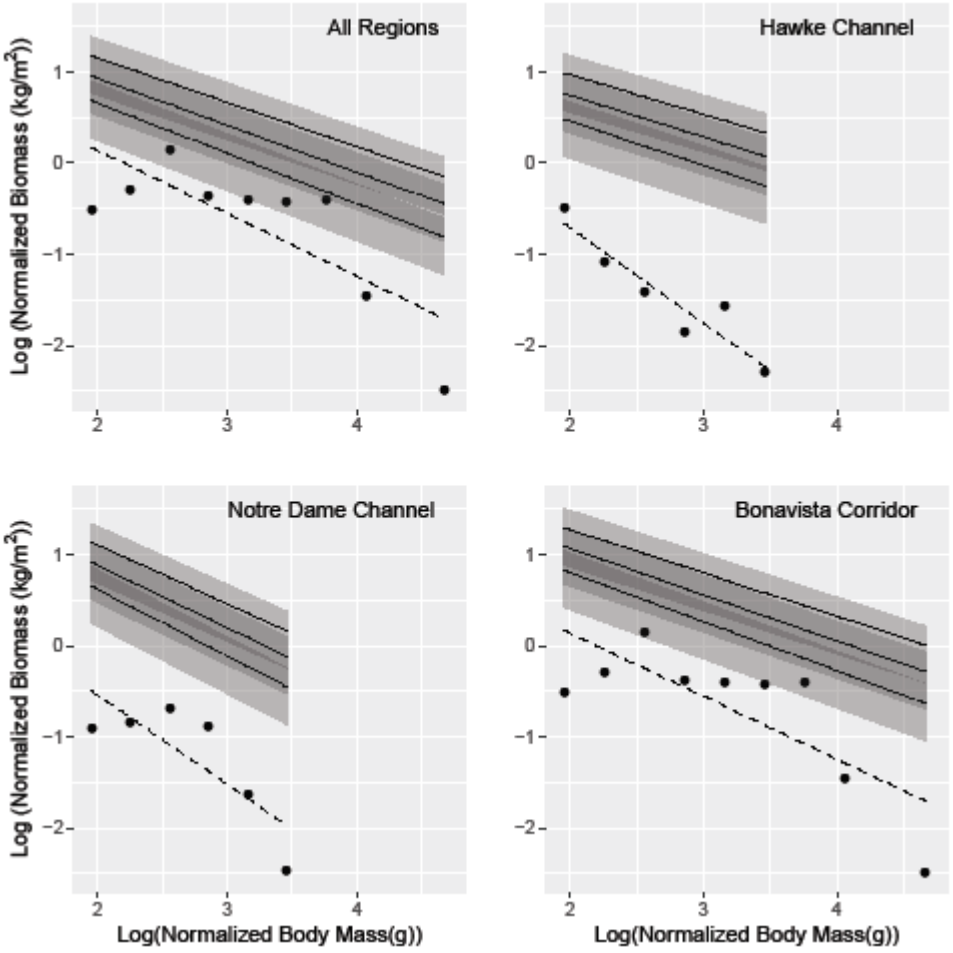

Fig. 4.3 Comparison of theoretical size structure (solid lines) at three levels of trophic efficiency and the empirical size structure regression (dotted line). Points represent the values from the empirical size spectra. The top theoretical line represents the highest trophic efficiency and the bottom the lowest trophic efficiency. The gray bars represent the range of annual primary productivity measured for this area for each theoretical line.

exception ($p = 0.50$). The steepest empirical slopes were observed in the Hawke and Notre Dame Channels and the shallowest slopes in the Bonavista Corridor (Table 4.3).

Variation among size categories and guilds

Variation among guilds underlies the overall community size structure. Based purely on biomass, the gadoids (predominantly Atlantic cod, *Gadus morhua*) represent the dominant guild in this community representing 77.7% of the fish biomass (pelagics

Table 4.2 Descending slopes of theoretical unexploited size spectra for three levels of ecotrophic efficiency across the whole sampled region 'Total Area' and within sub-regions.

Area	**Trophic Efficiency**		
	0.1	0.125	0.15
Total Area	-0.55	-0.52	-0.49
Hawke Channel	-0.48	-0.46	-0.43
Notre Dame Channel	-0.74	-0.68	-0.64
Bonavista Corridor	-0.54	-0.50	-0.48

Table 4.3 Descending slopes of empirical size spectra partitioned regions and fish guilds. Values in parentheses represent the r^2 of empirical size spectra.

Subset	**Descending Slope**
Total Area	-0.69 (0.59)
Hawke Channel	-1.04 (0.87)
Notre Dame Channel	-0.98 (0.65)
Bonavista Corridor	-0.69 (0.59)
Pelagics	-2.52 (0.83)
Gadoids	-1.02 (0.55)
Flatfish	-0.75 (0.61)
Elasmobranchs	-0.34 (0.15)
Demersal mesopredators	-1.47 (0.83)

represented 0.2%, flatfish 6.2%, elasmobranchs 0.8% and demersal mesopredators 15.1%). As such, gadoids were an important group in defining the community trends. Within this group Atlantic cod has received the most attention in this region. In the Bonavista Corridor, Atlantic cod represented 78.6% of the fish biomass and 39.6% by numbers in the trawl. These values decreased to 75.8% (biomass) and 16.1% (numbers) in the Notre Dame Channel and 28% (biomass) and 4.6% (numbers) in the Hawke Channel. The steepest slope was observed among the pelagics, which consisted primarily of barracudina (*Notolepis rissoi*) and myctophids (*Notoscopelus sp.* and *Benthosema glaciale*) (Table 4.3). The shallowest slopes were observed elasmobranchs, primarily thorny skate (*Amblyraja radiata*), which likely results from a relative deficit of data from small sample sizes. Flatfish, primarily American plaice (*Hippoglossoides platessoides*) and Greenland halibut (*Rheinhardtius hippoglossoides*), demersal mesopredators, primarily checkered Eelpout (*Lycodes vahli*) and redfish (*Sebastes sp.*), and gadoids also exhibited slopes steeper than that for the whole community (Fig 4.S4).

Theoretical vs Empirical Comparison

For all regions, the empirical biomass densities were typically a fraction of the unexploited ecosystem biomass densities (Table 4.4; Fig 4.4). For example, in the scenario of TE = 0.1, the combined size classes and regions within the empirical size

Table 4.4 Comparison of theoretical biomass density estimates across three trophic efficiencies with the biomass density estimate from the 2013 survey. The '±' values represent the range of primary productivity estimates investigated. Percent columns indicate the percent of the theoretical biomass densities at three TE values represented by the 2013 empirical biomass densities (presented in the final column).

Region	**Body Mass Class**	**TE = 0.1**		**TE = 0.125**		**TE = 0.15**		**2013 Biomass Density (g/m^2)**
		Biomass Density (g/m^2)	Percent (%)	Biomass Density (g/m^2)	Percent (%)	Biomass Density (g/m^2)	Percent (%)	
All Regions	All Sizes	77.2 ± 47.0	28.2	164.9 ± 100.1	13.2	306.8 ± 186.2	7.1	21.8
	< 4 kg	28.8 ± 17.6	60.3	59.2 ± 36.0	29.4	106.7 ± 64.7	16.3	17.4
	4 – 8 kg	25.6 ± 15.5	13.2	55.3 ± 33.6	6.4	104.0 ± 63.1	3.6	3.8
	>8 kg	22.8 ± 13.9	2.6	50.4 ± 30.6	1.1	96.1 ± 58.4	0.6	0.6
Hawke Channel	All Sizes	84.5 ± 51.3	6.2	179.21 ± 108.8	2.9	331.5 ± 201.3	1.6	5.2
	< 4 kg	29.3 ± 17.8	17.4	61.4 ± 37.8	8.3	114.3 ± 71.7	4.5	5.1
	4 – 8 kg	28.7 ± 17.4	0.3	60.2 ± 36.1	0.2	108.8 ± 63.9	0	0.1
	>8 kg	26.5 ± 16.1	0	57.7 ± 35.0	0	108.4 ± 65.6	0	0
Notre Dame Channel	All Sizes	50.0± 30.4	9.6	110.2 ± 66.9	4.4	210.9 ± 128.1	2.3	4.8
	< 4 kg	22.8 ± 13.8	20.6	47.5 ± 28.8	9.9	86.7 ± 52.7	5.4	4.7
	4 – 8 kg	15.0 ± 9.1	0.4	34.2 ± 20.8	0.2	67.0 ± 40.7	0.1	0.1
	> 8 kg	12.2 ± 7.4	0	28.5 ± 17.3	0	57.2 ± 34.7	0	0
Bonavista Corridor	All Sizes	90.5 ± 54.9	30.1	190.5 ± 115.7	14.3	350.2 ± 212.6	7.8	27.2
	< 4 kg	32.6 ± 19.8	65.7	66.2 ± 40.2	32.3	118.1 ± 71.7	18.1	21.4
	4 – 8 kg	30.3 ± 18.4	17.8	64.6 ± 39.2	8.8	116.7 ± 69.7	4.3	5.8
	> 8 kg	27.6 ± 16.8	2.9	59.7 ± 36.2	1.3	112.3 ± 68.2	0.7	0.8

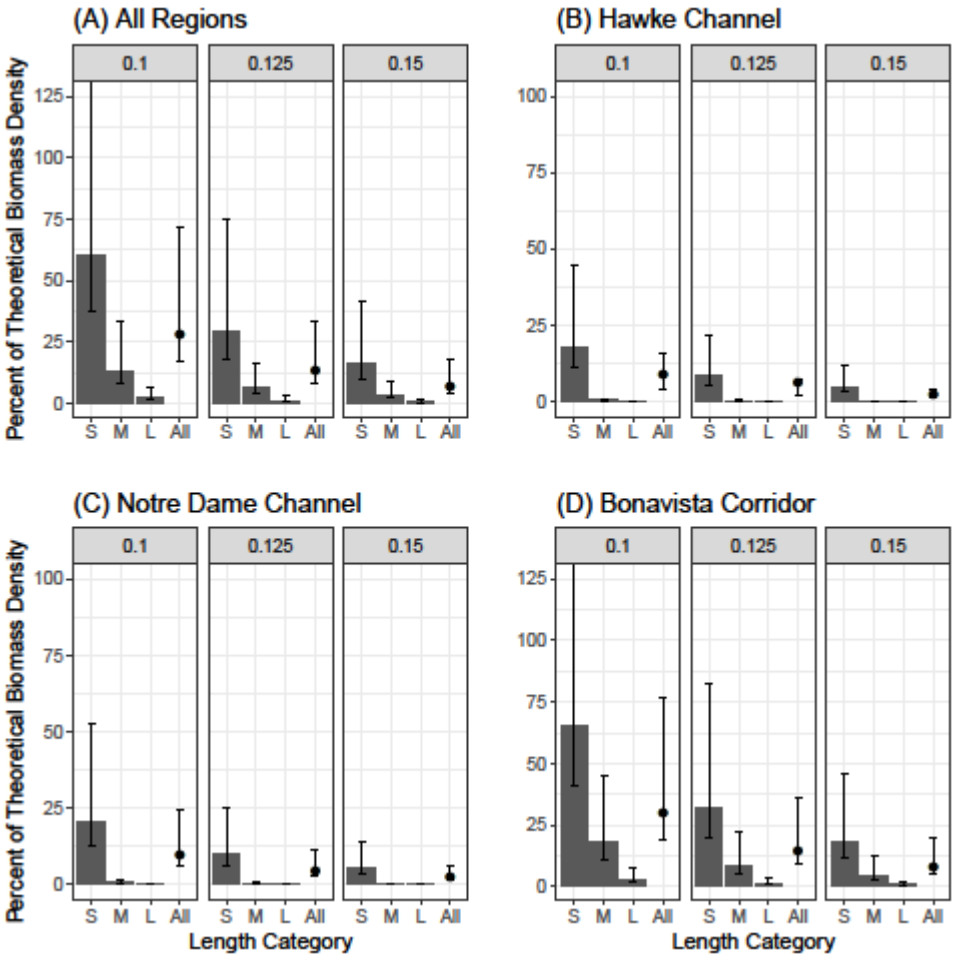

Fig. 4.4 Measured average biomass density as a percentage of the theoretical pristine biomass density by size class (S = small, M = medium, L = Large) and among pooled size classes "All" calculated for three levels of trophic efficiency (0.1, 0.125, 0.15) within the pooled regions (A), Hawke Channel (B), Notre Dame Channel (C), and Bonavista Corridor (D). Error bars represent the range of primary productivity estimates for this region.

spectrum represented only 27% (range 16.8-68.7%) of the theoretical biomass (Fig 4.4A). The only scenario where the empirical biomass fell within the range of the theoretical biomass was for the Bonavista Corridor when the lowest trophic efficiency and primary productivity were used (Fig 4.4D). Consistently across regions with increasing body masses the percentage of the theoretical biomass represented by the 2013 empirical biomass distribution decreased such that at the largest size category for the empirical distribution was between 0% (NDC and HC, where no large fish were sampled) and 14.4% (BC assuming TE = 0.1 and low primary productivity) of the theoretical distribution (Table 4.4, Fig 4.4). The mean trophic level at approximately 4.04 was not found to vary with region ($p = 0.18$) and did not differ significantly between the empirical and the theoretical analyses ($p = 0.29$).

Discussion

Quantifying the magnitude and timelines of marine fish community recoveries is challenged by appropriate characterization of baseline community conditions within long-exploited systems and changing ocean conditions (Pauly, 1995). Frequently, however, researchers establish biomass baselines using historical biomass estimates or data from nearby unexploited environments (e.g. Friedlander & DeMartini 2002, Sandin et al. 2008). Yet such baselines may still contain the remnants of anthropogenic effects such as human-induced climate change, pollution, etc. Historical baselines may furthermore represent ecosystems states are already fully exploited or even overexploited. Indicators at the community level of organization have been shown to be reliable and

robust to sampling variability and ecosystem differences, yet sensitive to ecosystem changes and are therefore useful for management (Fulton *et al.*, 2005). The empirical descending slopes and the biomass densities relative to a theoretical pristine size structure may function as ecological indicators (Jennings & Blanchard 2004, Shin et al. 2005). I therefore sought to approximate a theoretical pristine ecosystem size structure and respective biomasses based on ecological principles in order to provide an indicator of ecosystem recovery. The authors acknowledge that the present study represents only one year of data with no seasonality in the interest of avoiding potential temporal confounding variables. Though inspired by Jennings & Blanchard (2004), our work expands to include modern recommended approaches towards size spectra analysis as prescribed by Edwards et al. (2017), enhanced data on catchabilities, uncertainties around input parameter values (including primary productivity), and consideration of different fish guilds and size groupings to analyze a recovering ecosystem.

One of our most striking findings is the apparent distances between the contemporary biomass densities of small, medium, large, or pooled size classes and the theoretical biomass densities within and among regions of the Newfoundland and Labrador continental shelf (Figs 4.3-4.4). The only cases where the empirical spectrum was within range of the theoretical size spectra was for small fish in the situation where primary productivity and trophic efficiency were both assumed to be low. Since the moratoria on groundfish fishing (some of which were first initiated in1992), this region represents a recovering ecosystem following overexploitation, providing a system in which to address the unresolved question of whether and when cessation of fishing allows a community to

recover towards the unexploited abundance-body mass structure (Jennings & Blanchard 2004, Fung et al. 2013).

Important regional variations were also observed across both the empirical and theoretical size spectra. The Bonavista Corridor, the southern-most and most biodiverse of the regions analyzed (Chapter 2), was characterized by empirical spectra closest to the theoretical. This result aligns with observed recovery rates of Atlantic cod in these regions. It has been observed that the recovery rates in the Bonavista Corridor have proceeded faster than the recovery rates in either the Notre Dame Channel or the Hawke Channel (Lilly et al. 2008, Rose & Rowe 2015, DFO 2018). The Hawke Channel had the highest PPMR of all the regions studied, resulting in the shallowest descending slopes of the theoretical spectra. Such higher PPMRs are associated with shorter food chains such as one might expect from a predominantly invertebrate diet with relatively reduced food chain length (Jennings & Warr 2003).Although a wide range of PPMR is observed, they lie within the range of biologically feasible values (Nakazawa et al. 2011, Tsai et al. 2016). While the study area is treated as a single management unit for Atlantic cod (DFO 2018, 2019), a great deal of community heterogeneity is evident in this region. This regional heterogeneity in PPMR is consistent with complementary studies investigating stomach contents, trophic interactions, and isotopic niches (Krumsick & Rose 2012, Chapter 1 & 2). In light of the observed differences between these three focus regions, these regions are treated in this study as three separate ecosystems. These regions are not isolated from each other and migration, to a small extent, between these regions has been documented for Atlantic cod (Templeman 1979, Smedbol & Wroblewski 2002) and

Greenland halibut (Bowering, 1984). Yet despite this assumption, clear differences are observed among communities within sub-regions and as such they should not be considered functionally identical.

There are some potential limitations to the choice of samples and analyses. The present study utilized major Atlantic cod migration routes as a means of dividing the region based on biological characteristics, but this is by no means the only way these areas could be characterized. However, the sampled sub-regions are known to be representative of the broader stock distributions for dominant species as these species are known to aggregate along and within these offshore channels to spawn and escape cold, shallow shelf waters in spring (Fitzpatrick & Miller 1979). The spatio-temporal and taxonomic breadth of sampling may be seen as another potential limitation. The sampling extent assumes that the surveyed region is representative of the wider area. Further, this study represents only one year of fish size data with no characterization of potential seasonality in isotopic signatures, fish lengths, or species composition. A multi-year study of how these size spectra have changed with time (e.g. Daan et al [2005]) could provide further understanding of this ecosystem but was beyond the scope of this study. Furthermore, future analyses could assess whether these trends persist across seasons. Such consideration of temporal variability would be helpful to compare spatial vs. temporal variability within ecosystems with the potential for changes in prey dominance throughout the year.

As with Jennings & Blanchard (2004), invertebrates were not included in this study. Although invertebrates are an essential part of the ecosystem, the only species that I had

reliable body mass data for were *Pandalus* shrimp and snow crab. However all caught invertebrate species were smaller than the 64 g cutoff point presented (with the exception of jellies, sea anemones, and large snow crab). Despite our attempts to account for the lack of representation of smaller body sizes through the use of catchability estimates, our data of these smaller sizes were underrepresented and as such excluded from the analysis to avoid a potential bias. The present study also assumes a linear relationship between logged body mass and trophic level and as such a constant PPMR across sizes. Other studies, however, have indicated that PPMR would decrease with increased body mass (Barnes et al. 2010). I investigated this potential by fitting a number of potential functions to the plot and found that the fit was not improved over a simple linear function. As the PPMR could not be proven to be non-linear, I therefore also assumed a constant trophic efficiency through the relationship $TE = PPMR^{\beta+0.75}$, where β is the descending slope of the size spectrum (Barnes et al. 2010). The size spectra presented in this study also do not take into account asymptotic size of the species nor other species-specific factors which could influence size spectra such as variable assimilation efficiencies, daily intake, and search volume (Andersen & Beyer 2006, Persson & de Roos 2007). Finally, our analyses assume that size is the primary determinant of trophic level (Cohen et al. 1993, Romanuk et al. 2010), productivity (Banse & Mosher 1980, Schwinghamer et al 1986, Andersen et al. 2009), and biomass within the ecosystem (Kerr 1974, Blanchard et al. 2017, Edwards et al. 2017).

Our analyses also highlight the influence of trophic efficiencies and primary productivity estimates on theoretical size spectra. The trophic efficiency, combined with

the observed regional variation in PPMR, determined the rate of decline of theoretical size spectra. These descending slopes are vital to understanding anthropogenic influence on community size spectra, as steeper slopes indicate a heavier impact on communities (Shin et al. 2005, Blanchard et al. 2017). Trophic efficiency alone is difficult to estimate, being influenced by season (Gaedke & Straile 1994), water visibility (Irigoien et al. 2014), water temperature (Calbet et al. 2014), habitat complexity (Grabowski & Powers 2004), biodiversity (Gamfeldt et al., 2005), and predator and prey size diversity (Maxwell et al. 2010; García-Comas et al. 2016). Under unfavorable environmental conditions, we would anticipate a decrease in the trophic efficiency as more energy is invested into survival instead of productivity which in turn would also result in a steepening of the descending slope of the size spectra. A range of trophic efficiencies were presented to account for this uncertainty. The primary productivity determined the intercept of the theoretical size spectra. A range of estimates are provided corresponding with estimated annual primary production for these regions to control for potential seasonal variability. In addition to uncertainty in the measurement of this parameter, it is expected to vary from year to year as it is influenced by nutrient availability (Howarth 1988), water temperature (Taucher & Oschlies 2011), and vertical mixing (Neale et al. 1998). The range of primary productivities used may not represent a pristine historical environment but rather a modern estimate of primary production by which we can assess the impacts of long-term exploitation on fish communities. I therefore assumed that the primary production of the exploited ecosystem would not vary substantially from that of a theoretical unexploited one. The model also makes the assumption that fish production is

related to primary production, a relationship first proposed by Hrbáček (1969). From this relationship I obtained estimates of potential fish production to obtain our biomass estimates. This approach is naturally a simplification of reality as it does assume a high ecotrophic efficiency, a value which I do not presently have accurate estimations for though previous work has assumed a value of 0.95 for most species (Bundy et al. 2000).

Most size-based studies assume a single rate of decline of B with M for the entire community (Macpherson et al. 2002, Jennings & Blanchard 2004, Fock & Czudaj 2018), though there are exceptions (e.g. Daan et al. 2005). Newfoundland and Labrador size spectra, however, appear to exhibit different rates of decline for different sized fishes. The rate is lower and even comparable at smaller sizes, reaching a turning point and increasing rapidly between 1.4 and 5.5 kg. With this trend, the proportion of the theoretical biomass represented by the empirical distribution decreased with increasing size, consistent with other studies (Jennings & Blanchard 2004, Petchey & Belgrano 2010). Several factors contribute to the observed departure. Given that Altantic cod is the main contributing species for these larger size categories (96% by mass and 97% by numbers sampled in categories > 3.5 kg), this turning point occurs between the ages of 8 and 10 (Cadigan 2016). The cod at the observed turning point would therefore have been from a mid-2000s year class. A time delay is expected for communities to recover (Frank et al. 2011, Fung et al. 2013) and therefore this point may represent signs of recovery of fish populations. Furthermore, with fewer larger predators to consume the middle size-range fish, their biomass might be expected to be relatively higher due to a release from predation (Andersen & Rice 2010). The rapid decline in larger individuals and the small

percentage of the theoretical biomass represented by the observed biomass density is problematic as not all biomass can be considered equal in regard to recovery. The larger, older individuals are essential to rebuilding the overexploited fish stocks due to substantial contribution of large females to stock productivity (Longhurst 1998, Hixon et al. 2014), yet the size classes that could contribute most to recruitment and the recovery of fish stocks are the ones that are furthest away from the theoretical pristine distributions (Xu et al. 2013).

Among fish guilds, all (except the elasmobranchs) exhibit steeper slopes than the theoretical size-spectra (Tables 4.2-4.3). The gadoids, dominated by Atlantic cod (99% of gadoid biomass), was found to be a primary driver of the observed patterns of the community size structure, as it contributed the greatest proportion of sampled fish abundances and a wide range of sizes. Recent stock assessments for the spawning stock biomass of northern cod found the stocks to be at approximately 37% of the Limit Reference Point (DFO 2018). The steepest slope observed was the pelagic, driven by their high biomass in the smallest size class, then serving as forage fish prey for upper trophic predators. Flatfish and demersal mesopredator fish were found to exhibit slopes of intermediate magnitude. The vast majority of the demersal mesopredators were relatively small species (87.6% of the demersal mesopredator fish from the 2013 survey being less than 0.5 kg) with wolffish, redfish, and grenadiers rarely reaching larger sizes in this region (Templeman 1986, Power & Orr 2001, González-Costas 2010). The observed drop may therefore represent fewer species and fewer larger individuals. Similar to Atlantic cod, flatfishes have shown declines in abundance, being a fraction of

their historical levels (Healey et al. 2010, Morgan et al. 2013, DFO 2019). The observed size spectra are associated with reduced size structure and spawning stock biomass compared to historical flatfish populations as well as size structures in other regions, potentially arising from poor recruitment and high bycatch mortality (Morgan et al. 2013; DFO 2019). The only other guild that showed representation in various size categories were the skates as part of the elasmobranch guild. These fish were not as plentiful in numbers resulting in fairly scattered empirical size distributions with a flat slope.

Our consistent finding of low percentage of the theoretical biomass represented by the empirical spectra and low representation by the largest size classes is not unique to the Newfoundland and Labrador fish communities. Jennings and Blanchard (2004) found their North Sea empirical slopes to be seven to fifteen times greater than the theoretical; our study found the slopes to be only two to nine times greater. Their unexploited biomass densities, being between 0.8 and 9.2% of the theoretical biomass density (for TE of 0.125), were typically lower than those observed in this study. Other studies around the world found similarly small proportions of empirical biomass in exploited ecosystems compared to their own unimpacted biomass estimates, despite methodological differences (e.g. 1.5% in Friedlander & DeMartini 2002; 10% in Christensen et al. 2003; 5.3 – 21.5% in Myers & Worm 2003; 5% in Tang et al. 2003; 0.8 – 33.3 % in McClanahan et al. 2007; 25% in Sandin et al. 2008). Although the definition of un-impacted biomass varies among these studies as differing baseline determination methods were used, the overarching results of exploitation on fish communities are consistent. Our community analyses further illustrate that these differences between the observed state of community

size spectra and a pristine state can persist even following decades of fisheries moratoria. The combination of empirical size spectra and theoretical ones provide a basis from which we can establish indicators for this ecosystem. Many studies attempt to measure ecosystem recovery based on a previous ecological state, despite the fact that this state may already have been heavily impacted by human activity (e.g. Neubauer et al. 2013, Pedersen et al. 2017). Theoretical size-spectra, such as those presented in this study, seek to represent an ecosystem prior to anthropogenic interference (Hunter 1996), thereby providing a range of community reference points with which to direct and evaluate community rebuilding goals (Jennings & Dulvy 2005, Shin et al. 2005). Furthermore, these benchmarks may be used to set target biomass densities for recovering communities. Aiming for desired biomass densities targets at a set proportion of these theoretical densities may be helpful towards facilitating ecosystem recovery. The present study is not prescriptive in defining such targets as they require contributions from society, but these results illustrate the wide range of potential targets. Upon setting these targets, analysis of the present empirical size spectra slopes and biomass density estimates provide an indication of the distance to the desired target state from which managers can assess the effectiveness of population and ecosystem based management decisions.

Given the variables present within the model, factors that would promote recovery and increased observed biomass densities include:

(a) Increasing primary productivity to increase the intercept of the size spectra. This would also require that the extra production was consumed and depends on the nature of the links between members of the food web.

(b) Decrease PPMR to decrease the descending slope of the size spectra. In order to achieve this, diversity and size of prey would need to be increased to account for a range of sizes and availability of higher quality prey. The importance of prey diversity has been previously demonstrated for this system (Krohn et al. 1997, Sherwood et al. 2007). This point could feasibly be addressed by controlling fishing on key prey species thereby increasing the available diversity of prey.

(c) Increase trophic efficiency thereby decreasing the descending slope. This stage could be facilitated through, for example, increases of lipid-rich prey and/or prey which are more effectively digested. The recent "capelin hypothesis" limiting Atlantic cod recovery, stating that cod has not recovered due to a lack of capelin consumption and thereby relatively poor feeding, is more-or-less based on altering (b) and (c) (Rose & O'Driscoll 2002; Buren et al. 2014; Mullowney & Rose 2014).

(d) Modify future fishing practices such that larger fish are not preferentially removed. This removal steepens the descending slope via the larger, more productive individuals which are essential for population recovery (Birkeland & Dayton 2005, Hixon et al. 2013). We could feasibly modify of future fishing practices in order to increase the descending slopes of the size spectra.

The Newfoundland and Labrador fish communities are presently in a state recovering from overfishing in combination with changing ocean conditions which occurred in the late 1980s and early 1990s (Rice 2002, Pedersen et al. 2017). This combination resulted in a decrease in productivity of the ecosystem that exacerbated the effects of overexploitation and has since contributed to the observed lack of community recovery (Parsons & Lear 2001, Hillborn & Litzinger 2009). The removal of large fishes and subsequent expansion of lower trophic level populations led to ecosystem changes (Frank et al. 2006) and the addition of new invertebrate fisheries (Shrank 2005, Mather 2013). Contrary to recent portrayals of this ecosystem as one undergoing 'incipient recovery' relative to data collected in 1981 (Pedersen et al. 2017), our study shows that some sub-areas and size components have exhibited little recovery at the community level associated with continued low productivity. While a single species may recover relatively quickly, our results support that a damaged community may take decades to recover community and size-based characteristics (Frank et al. 2011, Fung et al. 2013). Conventional targeted fishing methods have resulted in selective removal of specific components of the ecosystem that have community-wide impacts (Pauly et al. 1998, Smith et al. 2011, Garcia et al. 2012, Essington et al. 2015). These impacts are exacerbated through the common practice of serial addition of low-trophic-level fisheries (Essington et al. 2006). Instead of heavily removing top predators, balanced harvesting has been proposed such that moderate removal of fish will take place across body sizes within the community and thereby ideally reduce damage to fish communities and allow for greater sustainable biomass yields (Garcia et al. 2012, Law et al. 2012, Rochet &

Benoît 2012). Such balanced harvesting reduces the impacts of fishing mortalities such that productivities approach more natural levels as well as improves ecosystem resistance to disturbances (Law et al. 2012). Furthermore, these practices function to protect the larger and more productive individuals (Birkeland & Dayton 2005, Hixon et al. 2013), an outcome that may also be facilitated through the use of properly selected marine protected areas (e.g. Barrett et al. 2007, Sherwood & Grabowski 2016, Kincaid & Rose, 2017). Though largely theoretical at this point (e.g. Garcia et al. 2012, Law et al. 2012, Law & Plank 2018), such balanced harvesting techniques have been partially implemented, unintentionally, on a small scale within several fisheries (Plank et al. 2014, Borges et al. 2016, Breen et al. 2016, Kolding et al. 2016, Plank et al. 2017). Although this approach to ecosystem based management has been criticized as unrealistic in their simplification of reality and the expected amount of micromanagement required for perfect implementation (Froese et al. 2015, Andersen et al. 2016, Reid et al. 2016), others argue it is still a viable solution if implemented properly (Borges et al. 2016, Howell et al. 2016, Reid et al. 2016, Plank et al. 2017). Discard bans have been proposed as a means to implement balanced harvesting, based on the idea that species with higher productivity will be more likely to be caught (Garcia et al. 2011, Borges et al. 2016), though this approach could have negative impacts for species with conservation concerns (Heath et al, 2014). As a moderate alternative, it has been recommended to gradually reduce fisheries discards to a level that would facilitate ecosystem stability (Fondo et al, 2015). In regard to first steps forwards towards a balanced harvesting approach, diversifying the catch, not only by species but also sizes caught, would distribute the

impact of fishing. In order to facilitate this shift, the implementation of a flexibly métier-based approach shows potential (Reid et al. 2016). This extra catch, however, has at present no market value. To facilitate cooperation of fishing fleets, either a market would need to be made for the unwanted bycatch (either through use as fish meal or through creative uses of presently unmarketable organisms) or a strong incentive would need to be provided to comply. By increasing the combinations of vessels and gear configurations to increase diversity of overall catches in addition to adequate reporting of catches, cooperation of fishing fleets, at least partial retention of discard, and an adaptive approach to reduce stress on species of concern (such as wolffish which are protected by the Canadian Species at Risk Act), we may approach a theoretical pristine ecosystem state and thereby limit damaging anthropogenic influences.

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Supplementary information

Table 4.S1 Identities and numbers of species sampled for stable isotope analysis in the 2015 survey by region and gear type.

Region	Gear	Species sampled (Number of individuals)
HC	Campelen 1800	American Plaice (21), Alligatorfish (9), Arctic Cod (5), Atlantic Cod (21), Atlantic Herring (2), Atlantic Hookear Sculpin (3), Atlantic Poacher (3), Blue Hake (1), Capelin (8), Checker Eelpout (9), Greenland Halibut (21), Marlin-spike (6), Moustache Sculpin (3), Myctophiid (*Benthosema*, 3), Myctophiid (*Notoscopelus*; 9), Redfish (21), Roughhead Grenadier (9), Smooth Skate (8), Snakeblenny (1), Thorny Skate (18), Threebeard Rockling (1), White Barracudina (3), Witch Flounder (3)
NDC	Campelen 1800	American Plaice (16), Arctic Cod (15), Atlantic Cod (6), Atlantic Herring (1), Atlantic Hookear Sculpin (1), Capelin (1), Greenland Halibut (9), Moustache Sculpin (3), Redfish (12), Thorny Skate (2), White Barracudina (2), Witch Flounder (2)
	Mid-water Trawl	American Plaice (5), Arctic Cod (2), Atlantic Cod (14), Atlantic Herring (8), Capelin (8), Greenland Halibut (7), Myctophiid (*Benthosema*, 3), Myctophiid (*Notoscopelus*; 9), Redfish (9), Thorny Skate (1), White Barracudina (1), Witch Flounder (1)
BC	Campelen 1800	American Plaice (21), Alligatorfish (9), Arctic Cod (17), Atlantic Cod (21), Atlantic Herring (9), Atlantic Hookear Sculpin (3), Atlantic Poacher (9), Capelin (9), Checker Eelpout (10), Fourline Snakeblenny (2), Greenland Halibut (21), Longfin Hake (1), Marlin-spike (9), Moustache Sculpin (3), Myctophiid (*Notoscopelus*; 9), Redfish (22), Smooth Skate (1), Snakeblenny (1), Thorny Skate (21), Threebeard Rockling (5), White Barracudina (4), Witch Flounder (13)

Table 4.S2 Catchabilities and length-weight relations for all analyzed species. In cases where weights of individual fish were obtained, those were used and no length-weight relation was required. The first reference is for the length-weight relation (unless all individuals were weighed, in which case relation from the literature was required) and the second reference is for the catchability.

Species	Scientific Name	Length-Weight Relation	Catchability	References
Alligatorfish	*Aspidophoroides monopterygius*	$W = 0.0029 * L^3$	0.25	Alpoim *et al.*, 2002; Jennings *et al.*, 2002
American Plaice	*Hippoglossoides platessoides*	$W = 0.0036 * L^{3.305}$	See Fraser *et al., 2007*	Paz & Román, 1997
Anglerfish	*Oneirodes macrosteus*	All Individuals Weighed	0.021	Walker *et al.*, 2017
Arctic Cod	*Boreogadus saida*	All Individuals Weighed	$4.8585 * \frac{e^{(-4.575+0.0783*L)}}{1+e^{(-4.575+0.0783*L)}}$	Harley & Meyers, 2001
Argentine	*Argentina silus*	All Individuals Weighed	0.0658	Harley *et al.*, 2001
Atlantic Cod	*Gadus morhua*	$W = 0.0081 * L^{3.044}$	$7.2277 * \frac{e^{(-5.04+0.138*L)}}{1+e^{(-5.04+0.138*L)}}$	Árnason *et al.*, 2009; Harley & Meyers, 2001
Atlantic Halibut	*Hippoglossus hippoglossus*	All Individuals Weighed	$4.3368 * \frac{e^{(-4.41+0.109*L)}}{1+e^{(-4.41+0.109*L)}}$	Harley & Meyers, 2001
Atlantic Herring	*Clupea harrengus harrengus*	$W = 0.0097 * L^{2.96}$	See Walker *et al.*, 2017	Wigley *et al.* 2003
Atlantic Hookear Sculpin	*Artediellus atlanticus*	$W = 0.02 * L^{2.85}$	0.25	Greenstreet *et al.*, 2012; Jennings *et al.*, 2002
Atlantic Lumpfish	*Cyclopterus lumpus*	All Individuals Weighed	0.25	Jennings *et al.*, 2002
Atlantic Poacher	*Agonus decagonus*	$W = 0.0043 * L^{2.98}$	0.25	Alpoim *et al.*, 2002; Jennings *et al.*, 2002
Atlantic Wolffish	*Anarhichas lupus*	$W = 0.0053 * L^{3.077}$	0.4067	Templeman, 1986; Harley *et al.*, 2001

Capelin	*Mallotus villosus*	$W = 0.0042 * L^{3.11}$	0.08	Alpoim *et al.*, 2002; O'Driscoll *et al.*, 2002
Checker Eelpout	*Lycodes vahlii*	$W = 0.0017 * L^{3.27}$	0.471183	Alpoim *et al.*, 2002; Walker *et al.*, 2017
Daubed Shanny	*Lumpenus maculatus*	$W = 0.0091 * L^{2.335}$	0.25	Greenstreet *et al.*, 2012; Jennings *et al.*, 2002
Greenland Halibut	*Reinhardtius hippoglossoides*	$W = 0.005 * L^{3.1804}$	$4.3368 * \frac{e^{(-4.41+0.109*L)}}{1+e^{(-4.41+0.109*L)}}$	Román & Paz, 1997; Harley & Meyers, 2001
Lightless Loosejaw	*Malacosteus niger*	All Individuals Weighed	0.25	Jennings *et al.*, 2002
Longfin Hake	*Urophycis chesteri*	$W = 0.0104 * L^{2.8226}$	0.303	Paz & Román, 1997; Harley *et al.*, 2001
Marlin-spike	*Nezumia bairdi*	$W = 0.0254 * L^{2.89}$	0.25	Alpoim *et al.*, 2002; Jennings *et al.*, 2002
Moustache Sculpin	*Triglops murrayi*	$W = 0.0032 * L^{3.46}$	0.25	Alpoim *et al.*, 2002; Jennings *et al.*, 2002
Myctophiid	*Notoscopelus* sp. & *Benthosema glaciale*	$W = 0.0054 * L^{3.08}$	0.25	Alpoim *et al.*, 2002; Jennings *et al.*, 2002
Northern Wolffish	*Anarhichas denticulatus*	$W = 0.017 * L^{2.92}$	0.4067	Alpoim *et al.*, 2002; Harley *et al.*, 2001
Redfish	*Sebastes* sp.	$W = 0.0247 * L^{2.9364}$	See Walker *et al.*, 2017	Paz & Román, 1997
Roughhead Grenadier	*Macrourus berglax*	$W = 0.1851 * L^{2.7542}$	0.25	Paz & Román, 1997; Jennings *et al.*, 2002
Sea Tadpole	*Careproctus reinhardti*	All Individuals Weighed	0.25	Jennings *et al.*, 2002
Shorthorn Sculpin	*Myoxocephalus scorpius*	$W = 0.0138 * L^{3.06}$	0.4933	Fishbase.org; Harley *et al.*, 2001

Smooth Skate	*Raja senta*	$W = 0.02 * L^{2.85}$	0.0799	Paz & Román, 1997; Harley *et al.*, 2001
Spotted Wolffish	*Anarhichas minor*	$W = 0.0053 * L^{3.1719}$	0.4067	Paz & Román, 1997; Harley *et al.*, 2001
Snakeblenny	*Lumpenus lumpretaeformis*	$W = 0.0164 * L^{2.09}$	0.25	Alpoim *et al.*, 2002; Jennings *et al.*, 2002
Stout Sawpalate	*Serrivomer beani*	All Individuals Weighed	0.25	Jennings *et al.*, 2002
Thorny Skate	*Raja radiata*	$W = 0.0436 * L^{2.8611}$	0.0799	Paz & Román, 1997; Harley *et al.*, 2001
Three-beard Rockling	*Gaidropsarus ensis*	$W = 0.007 * L^{2.977}$	$8.7398 * \frac{e^{(-3.47+0.0916*L)}}{1+e^{(-3.47+0.0916*L)}}$	Alpoim *et al.*, 2002; Harley & Meyers, 2001
White Barracudina	*Notolepis rissoi*	$W = 0.0003 * L^{3.58}$	0.25	Alpoim *et al.*, 2002; Jennings *et al.*, 2002
White Hake	*Urophycis tenuis*	$W = 0.0043 * L^{3.153}$	0.333	Beacham & Nepsezy, 1980; Harley *et al.*, 2001
Witch Flounder	*Glyptocephalus cynoglossus*	$W = 0.0008 * L^{3.497}$	$4.3368 * \frac{e^{(-4.41+0.109*L)}}{1+e^{(-4.41+0.109*L)}}$	Bowering & Stansbury, 1984; Harley & Meyers, 2001
Wolf Eelpout	*Lycenchelys verrilli*	All Individuals Weighed	0.25	Jennings *et al.*, 2002
Wrymouth	*Cryptacanthodes maculatus*	All Individuals Weighed	0.25	Jennings *et al.*, 2002
Viperfish	*Chauliodus sloani*	All Individuals Weighed	0.25	Jennings *et al.*, 2002

Table 4.S3 Primary productivity estimates for the Newfoundland and Labrador shelf communities.

Region	Years	Annual Primary Productivity Estimate ($g\ C\ m^{-2}y^{-1}$)	Study
Newfoundland-Labrador Shelf	1979-1986	540	Longhurst *et al.*, 1995
Grand Banks	1980-1981	186-194	Prasad & Haedrich
Newfoundland-Labrador Shelf	1980-1993	156 - 482	Bundy *et al.*, 2000
Newfoundland-Labrador Shelf	1993	150 - 300	Aquarone & Adams, 2008
Newfoundland-Labrador Shelf	1998-2002	132 - 190	Conti & Scardi, 2010
Newfoundland-Labrador Shelf	2001	440	Pepin & Mailet, 2002
Newfoundland-Labrador Shelf	2006-2010	241	Guijarro *et al.*, 2016

Table 4.S4 Sample sizes by year within size categories. Fishes sampled in 2013 were measured for the biomass composition and fish sampled in 2015 were sampled for stable isotope analysis.

Year	Region	Size	Number of Fish
2013	Hawke Channel	< 4 kg	654
		4 – 8 kg	2
		> 8 kg	0
	Notre Dame Channel	< 4 kg	708
		4 – 8 kg	1
		> 8 kg	0
	Bonavista Corridor	< 4 kg	5741
		4 – 8 kg	404
		> 8 kg	27
2015	Hawke Channel	< 4 kg	179
		4 – 8 kg	10
		> 8 kg	1
	Notre Dame Channel	< 4 kg	113
		4 – 8 kg	5
		> 8 kg	0
	Bonavista Corridor	< 4 kg	213
		4 – 8 kg	7
		> 8 kg	1

Fig. 4.S1 Flow chart of the methods used in this study. Green boxes represent values that were measured by the authors, purple boxes represent values obtained from the literature, blue boxes represent calculations conducted by the authors, and black boxes represent the outputs of the model.

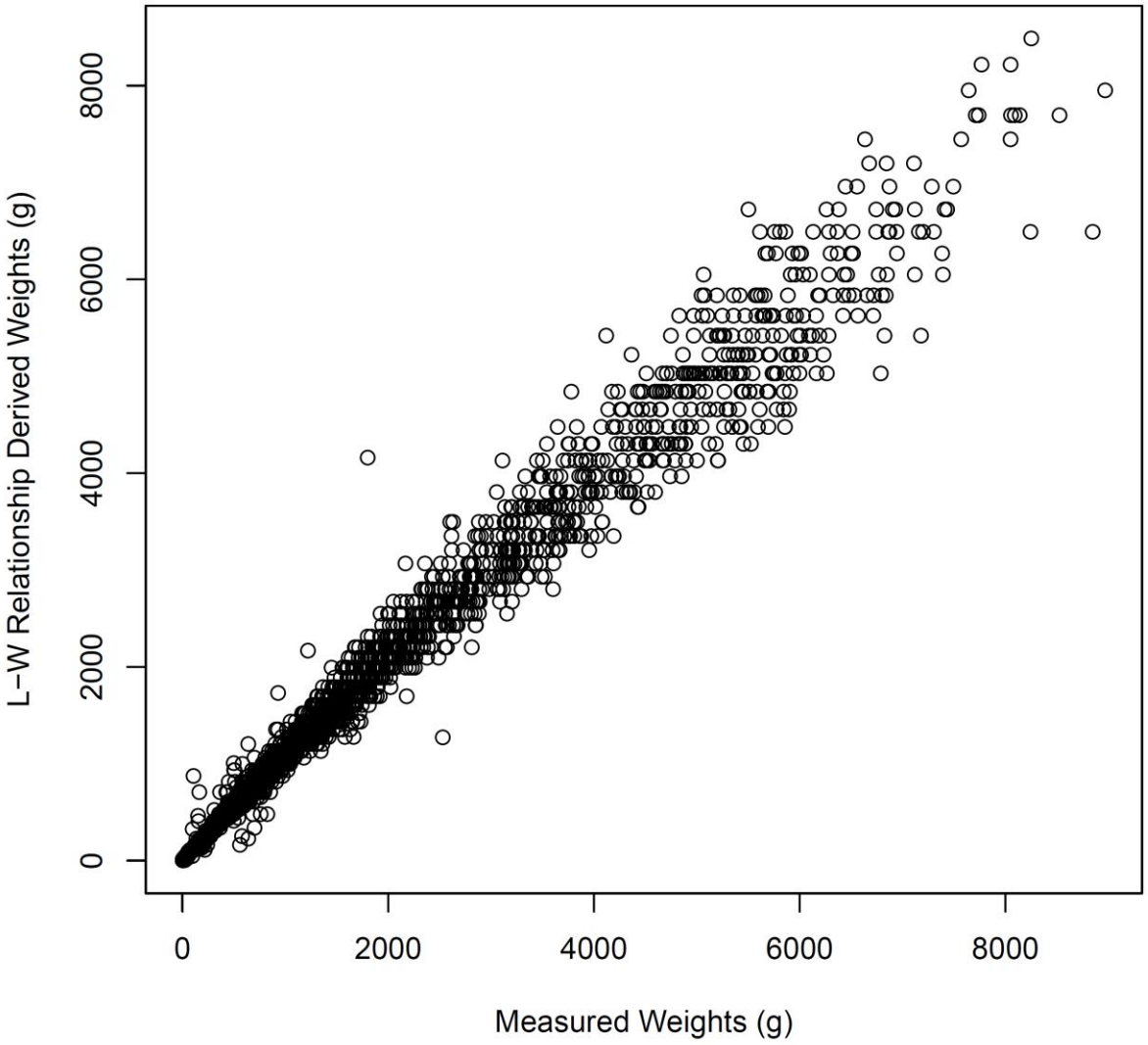

Fig. 4.S2 Comparison of measured weights to those derived from published species-specific length-weight relationships for individuals which were weighed in the field. Although deviations exist, a linear relationship with a slope of 1 is observed, indicating the relationships are overall adequate approximations.

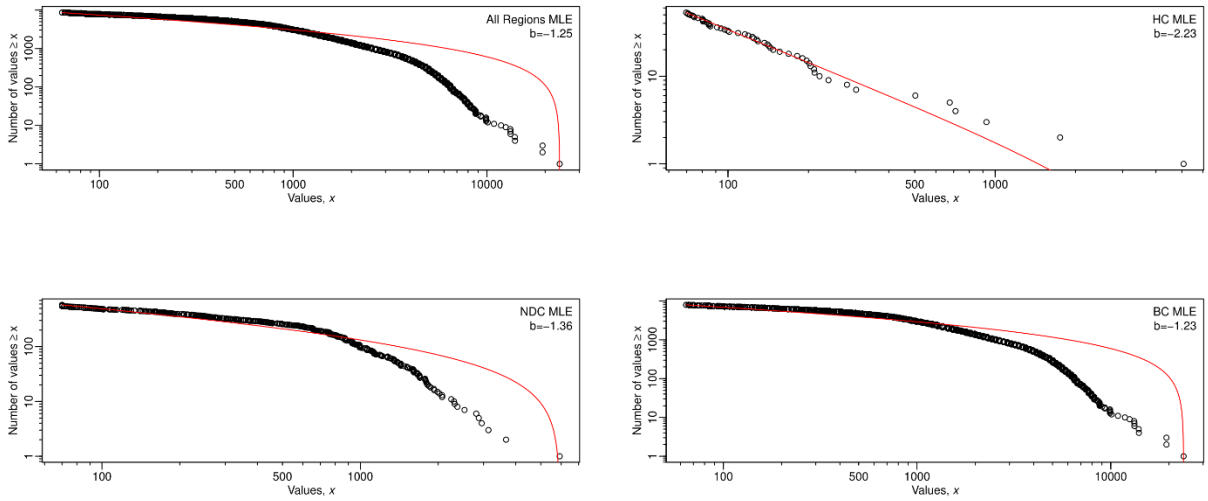

Fig. 4.S3 Maximum Likelihood Estimate method for estimating power-law distributions (lines overlying the empirical data from three regions and pooled regions) based on code provided in Edwards et al. (2017). The differences between MLE methods and empirical data demonstrate that, as indicated by Vidondo et al. (1997), power-law distributions are not appropriate for all data sets.

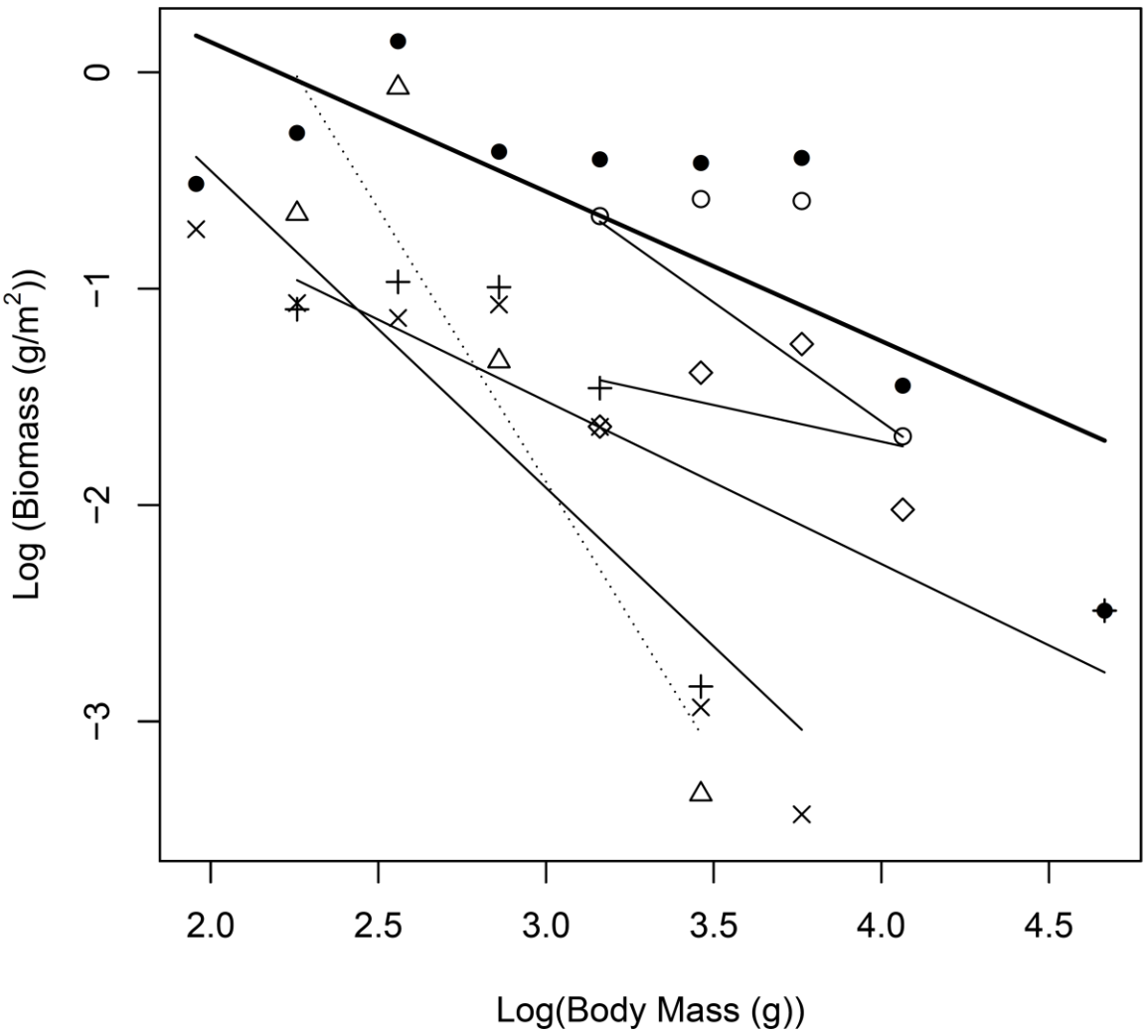

Fig 4.S4 Individual size spectra for each fish guild (● for all fish, ○ for cod, + for flatfish, Δ for pelagics, ◊ for elasmobranchs, and x for demersal mesopredators). Dashed lines represent significant deviations from the community spectrum and solid lines represent non-significant differences in slope.

Chapter 5: Conclusion

Summary

The focus of this research was to use knowledge of stable isotope ecology to address new questions regarding the current state of Newfoundland and Labrador's marine ecosystems. These results contribute to increasing our understanding of modern ecosystem dynamics as well as provide information that could fuel the next generation of ecosystem-based models and management decisions. The Newfoundland marine ecosystem is dynamic with numerous factors influencing species assemblages including current oceanographic regimes (Rose et al. 1995, Han 2006), anthropogenic activities (Gomes et al. 1995, Hamilton et al. 2004), climate change (Halliday & Pinhorn 2009), and population variation driven by trophic cascades (Lilly et al 2000, Bundy 2001, Carscadden et al. 2001). Understanding of present and past ecosystem dynamics are therefore essential for understanding the impacts that these factors may have in regard to future potential ecosystem changes (Drinkwater 2005, Denman et al. 2011, Jackson et al. 2011).

To begin the investigation into the local food webs, I began by quantifying isotopic niche overlap within important, recovering Northwest Atlantic marine fish communities through analyses of $\delta^{15}N$ and $\delta^{13}C$ muscle tissue signatures from seven abundant fish species. The specific objectives of this study are to: (a) determine the influence of species richness and diversity (both fish communities and their prey) on the community trophic structure among three regions, and (b) assess community-level trophic niche overlap

metrics, including the influences of ontogenetic variation on these metrics. Key results from this study include:

- Fish and prey diversity were found to decrease with latitude, indicating environmental heterogeneity across the study region.
- With decreasing prey diversity, increased overlap in trophic niche was observed. In addition, with this decreased diversity we observed decreased distances to the community centroid and mean distance to nearest neighbor within isotope biplot isotope space.
- Except for Atlantic cod, all analyzed species trended towards the community centroid with ontogeny presumably as they become more effective predators due to such factors as increased gape size and increased ability to pursue prey.
- Although most studies analyze a species by combining life stages, our results reveal the importance of considering variable trophic niches filled over the size range within species. Consideration of these ontogeny-driven trophic niche changes reveals differences in community niche overlaps and potential competitive interactions. This has not been revealed previously using stable isotope Bayesian ellipses.
- Atlantic cod was clearly a top predator in this ecosystem, although the extent to which its trophic niche overlapped varied spatially as a function of prey diversity. This observation could hint at a contributing factor to variable cod recovery rates within this region: competition for food resources.

By determining the isotopic niche occupied by various predatory fish species in chapter 2, I was able to approximate the trophic niche these species occupy. However, while Bayesian ellipses may provide an indication of potential competition, it is not sufficient to determine such an interaction as variable fractionation coefficients and potential prey combinations could result in an observed isotopic signature. The relative diet proportions of different prey species was therefore investigated to determine whether the observed Bayesian overlap was based on common diets and if so what major nutrient pathways exist within these ecosystems.

I then proceeded to investigate specific species interactions and the underlying function of the food web. Toward this end, I measured the stable isotopic values of all species (except protected species and species which were difficult to obtain isotope values such as scyphozoans) caught in trawls and plankton tows. My purpose was threefold: (a) to construct simplified marine food webs based on the results from stable isotope mixing models supplemented by stomach contents data to determine how they vary spatially, (b) analyze spatial variation in the diets of abundant and economically important species in the study regions, and (c) discuss how these results relate to spatial variation in ontogenetic niche overlap and size-spectra recovery. Among the major results of this chapter were:

- Key prey species in the Bonavista Corridor were found to be copepods, hyperiids, and polychaetes. Fish prey were also more common in this region than the other two regions. In the Notre Dame Channel, hyperiids, bivalves, and shrimp were

found to be key prey species. In the Hawke Channel, shrimp was frequently a dominant prey item in predator diets with notable contributions of polychaetes.

- Northern regions, known to have lower diversity, showed increased connectance and shorter food chain lengths in association with the observed increased contribution of benthic invertebrates, particularly northern shrimp.
- The benthic portion of the food web was found to increase relative to the pelagic portions of the food web with latitude which has been attributed to heavily impacted marine communities.
- Atlantic cod diet was found to be highly varied in the Bonavista Corridor, but quickly became dominated by shrimp and crab in the northern regions. Greenland halibut were found to consumed primarily zooplankton species with significant contributions of capelin in both the Bonavista Corridor and the Notre Dame Channel which was replaced with shrimp and gammarids in the Hawke channel. Redfish diet was found to consist of shrimp and pelagic invertebrates, though the proportion of shrimp increased with both size and latitude.

Using isotope mixing models I was able to ascertain details of nutrient flow through the ecosystem. Knowledge of such key species interactions is paramount for understanding ecosystem functioning and for shifting toward ecosystem-based management. However, in order to assess ecosystem recovery, we need to establish community-based indicators, which provided the foundations for chapter 4.

My final chapter is based on deriving ecosystem indicators for modern Newfoundland and Labrador shelf fish community rebuilding through the construction of theoretical

size-spectra constructed from predator-prey body mass ratios, primary productivity estimates, and a range of trophic efficiencies. These theoretical 'pristine' size spectra are then compared to empirical size spectra to evaluate the present state of the community. My purpose was threefold: (a) to assess how much biomass at size we should observe in an ideal theoretical situation, (b) to determine how far the current biomass density estimates are from a theoretical unexploited size structure, and (c) to determine if the influence of overexploitation on the community size structure remain evident over two decades after the implementation of fisheries moratoria. Among the major findings were:

- The descending slopes of the empirical size spectra remain between 1.25 and 2.42 times steeper than the theoretical ones with biomass densities of larger size classes decreasing faster than smaller size classes.
- The empirical size structure represented a small portion of the theoretical one, ranging between from 0 to 32.3% for medium trophic efficiencies.
- The empirical size structure in northern regions with the lowest observed recovery rates were the furthest from the theoretical size spectra.
- While most prior indicators for recovery have been established based on recorded historical levels, the presented community-level indicators illustrate the current gap between current size spectra and what could theoretically be observed.
- Balanced harvesting is a potential approach that could decrease the pressure on larger individuals and overall increase the descending slope of the empirical size spectrum.

While these estimates are not designed to be used as targets, which include the socioeconomic considerations, the presented distributions and indicators provide a novel means to provide community-based information to guide management decisions.

Although the size-based approach provides a convenient means by which we can monitor the ecosystem and potentially advise management plans, we cannot ignore the fact that species identity is still important (Petchey & Belgrano 2010, Rudolf et al. 2014, Griffin & Silliman 2018). The ecosystem would not benefit from the preferential removal of certain species at certain sizes simply to accommodate economic convenience. Accomodations need to take into account such factors as relative biomass and rate of reproduction of the species as well as special consideration for species at risk. Furthermore, we need to consider the interactions with other species and potential ontogenetic variation (Werner & Gilliam 1984, van Leeuwen et al. 2014). The first two chapters of this thesis provided insights into some of the complexities of such species interactions.

Species do not exist in isolation and as such should not be treated as a single species. I provided insights that a given fish species are not always fulfilling the same role within the ecosystem. The isotopic niche that a species fills will likely change over their lifetime as well as spatially as a result of spatial heterogeneity of prey availability. I demonstrate that a large portion of this variability is dependent on the ecosystem, diet diversity, and the relative proportion of the benthic and pelagic portions of the food web. The combination of all these elements may naturally be overwhelming, and as such, it may be difficult to implement ecosystem approaches toward management (Slocombe 1993, Tallis

et al. 2010). While the development and perfect implementation of policies based on the previously mentioned ecosystem considerations would be the ideal situation, this approach has been criticized as too ambitious to instantly apply (summarized in Murawski 2007, Patrick & Link 2015). Instead, stock assessment recommendations could be gradually modified to incorporate increasing amounts of ecosystem considerations such as species interactions and community size spectra. Such steps towards improving our approaches towards ecosystem health will help to facilitate ecosystem recovery from overexploitation.

While discussing ecosystem recovery, a question often arises: how do we designate a system as recovered? Prior studies point to a time within living memory when the populations were at the least more productive (e.g. Neubauer et al. 2013, Rose & Rowe 2015, Pedersen et al. 2017). This bias has resulted in what has been termed the "shifting baseline syndrome" such that each generation of fisheries scientists accepts the baseline stock sizes to be those at the start of their careers (Pauly 1995, Pinnegar & Engelhard 2008). However, even these benchmarks are substantially lower than population biomass estimates prior to extensive fishing pressures (Steele & Schumacher 2000, Rose 2004). Considering the fisheries-induced evolution observed in many stocks (Kuparinen & Merilä 2007, Enberg et al. 2009, Heino et al. 2015) as well as shifted focus of fishing efforts (Pauly et al. 1998, Tromeur & Loeuille 2018), do we try to return to a historical state or attempt to adapt to the present state? The present research works under the assumption that fisheries-induced evolution has made it unlikely for fish populations to return to a prior state of life history characteristics and therefore seeks to assess trophic

interactions and size spectra based on the current state of the ecosystem. Naturally, the prevention of further fisheries-induced evolution should be a priority, one that may be helped with the implementation of the balanced harvesting approach promoted in this research (Law & Planck 2018). However, it should be noted that complex ecosystems will often exhibit multiple stable states (e.g. Lewontin 1969, May 1997, Beisner et al. 2003, Conversi et al. 2015) and therefore the current state could be temporary. Continued ecosystem survey and adaptive management to assess shifts in community biomass, trophic interactions, and life history parameters of its members is therefore required to best account for future ecosystem changes and climate change (Pershing et al. 2015).

Limitations of Presented Analyses

The use of stable isotopes as a tool for the study of food web dynamics has been increasing almost exponentially since their use in ecology was first discovered (Crawford et al. 2008, Phillips et al. 2014). Given their recent popularity, stable isotopes have developed an image of being a sort of "magic" tool for resolving diet information. Nevertheless, while undoubtedly a useful tool, stable isotope analyses, as with other methodologies used to analyze trophodynamics, do of course come with numerous limitations but can be most useful when applied concurrently with other methodologies such as stomach content analysis and fatty acid analysis (Gannes et al. 1997).

Firstly, a number of biological and non-biological processes (Newsome et al. 2007, Jackson et al. 2011) determines the stable isotope values of a predator. The focus of most studies using stable isotopes is to determine the trophic linkages and is thought to be

the primary determining factor of a predator's isotopic value (Bearhop et al. 2004). Yet many other factors will lead to variability surrounding this measure. The fractionation coefficients alone are responsive to a number of different factors including prey identity (Vander Zanden & Rassmussen 2001, Hussey et al. 2014), temperature (Barnes et al. 2007, Sweeting et al. 2007), feeding rate (Barnes et al. 2007), growth (Cerling et al. 2007), prey isotope values (Caut et al. 2008, Caut et al. 2009), protein and fat content of the prey (McCutchan et al. 2003, Robbins et al. 2005), and tissue type (Pinnegar & Polunin 1999, MacNeil et al. 2004, Sweeting et al. 2007). To account for this limitation, I initially attempted to determine predator-species dependent fractionation coefficients estimated from the stomach content information obtained. This approach, however, did not produce reasonable fractionation estimates for many of the species likely due to low stomach sample sizes and that stomachs represent only a snapshot in time while stable isotopes represent the diet over the span of months (Fry 1988, Lorrain et al. 2002, MacNeil et al. 2006, Olson et al. 2010). In these cases, a published estimate was used in chapters 2 and 3. Although I did account for variation in the carbon and nitrogen content among prey items, this introduces an additional assumption that the prey are digested to approximately equal extent. As muscle tissue was used as a measure of the isotopic value, these measures do not take into account tissue-specific isotopic variation. Furthermore, some prey, such as the various zooplankton taxa, were ground whole for the isotopic analysis due to the impossibility of extracting muscle tissue.

Many studies extract lipids prior to isotope analysis (e.g. Hobson & Clark 1992, Post et al. 2000) using a methanol-chloroform solution (Folch et al. 1957) as δ^{13}C will

fractionate during lipid synthesis (DeNiro & Epstein 1977) and lipid content will vary substantially among species (Post 2000). However, such lipid removal has been shown to create derived products which will alter the δ^{15}N signature in ways that are often difficult to predict (Pinnegar & Polunin, 1999; Sotiropoulos *et al.*, 2004; Logan *et al.*, 2008), resulting in us using a mathematical correction to correct for the δ^{13}C based on variable lipid content (Ricklefs & Travis 1980, Post et al. 2007). The correction, however, assumes a mathematical relation that may be a simplification of reality and result in a potential bias in the isotopic values used in this thesis when comparing to other studies that opted for lipid removal or no lipid correction at all.

In addition to the assumptions associated with stable isotope analysis, a number of assumptions were made regarding parameter estimates used in this research. In addition to the fractionation coefficients previously mentioned, such parameters as primary productivity and trophic efficiency could not be actively measured or estimated from the data that was collected. Although estimates for these values were often taken from the literature, given time and resources more accurate estimates for the local ecosystems would have been optimal.

Another primary limitation of this research was the scope of the sampling. The samples were collected opportunistically on ecosystem surveys conducted by CFER aboard the RV Celtic Explorer. The regions were chosen in the interest of not interfering with other presently unpublished work conducted by previous members of our group on the Grand Banks and south coast of Newfoundland. However, because of these regional restrictions, there were only two years of data that could be used. However, one year did

not adequately sample potential invertebrate prey and the other year lacked trawl catch data due to reasons beyond my control. As a result, only two years of data were usable in the present research. Furthermore, only the spring season was represented. Although the Department of Fisheries and Oceans does conduct their own survey in this region during the fall, the exact details of the sampling procedures that are undergone during these surveys are not released publicly and personal communication has brought into question the potential comparability of the surveys. As sampling was opportunistic within the scope of the CFER surveys, there was little to no opportunity for potential additional sampling. Additional samples from a grab sampler and additional plankton tows would have provided additional information on potential prey, making the estimates of the prey isotopic values more precise. Furthermore, more diligent measurement of invertebrate prey such that we would be able to obtain a mass for each individual would allow us to incorporate invertebrates into the community size spectra. The trawl samples were additional collected with a Campellen trawl with additional contributions from a midwater trawl for the collection of stable isotope samples. This gear is more efficient at capturing smaller members of the species presented in this study (Walsh & McCallum 1996). Furthermore, given that tow duration was not constant, there is the possibility that the trawl simply did not collect larger individuals with higher swimming endurance. A simple analysis of the maps presented in this thesis reveal that the sampling effort was also not evenly spread across the region. The Bonavista Corridor was the primary region of focus for a number of cod-focused publications resulting from the ecosystem surveys (Rose & Rowe 2015, Rose & Rowe 2018). As the other regions were of relatively less

interest, the sampling was reduced. Additionally, given the focus on cod recovery on these surveys, there was a distinct focus on the three major trenches thought to be important to spring cod migration (Rose, 1993) with little to no coverage of the banks existing in between (the Funk Island Bank and the Hamilton Bank). The trenches are thought to provide warm water refuges for fish in this region (Rose 1993, Colbourne et al. 2013) and therefore the benthic ecosystem dynamics are likely to be quite different on these banks.

In any study of foodwebs, it is important to consider the members at the base of the foodweb in order to resolve of the rest of the community. Frequently in studies involving stable isotope ecology, a reference species is provided of a known trophic level, typically a known herbivorous species (e.g. Carscallen et al. 2012) or a large, sessile organisms such as a bivalve (e.g. Lake et al. 2001, Jennings & Warr 2003) or a gastropod (Post et al. 2000). The copepod species *Calanus finmarchicus* was selected as a baseline species as it was a lower food web species of known trophic level, was sampled in all regions, and has been recommended as a potential baseline species in other food webs (Hansen et al. 2012). However, the use of this species is not without its assumptions. During phytoplankton blooms, δ^{13}C and δ^{15}N of phytoplankton have been reported to increase which in turn will increase the isotopic values in zookplankton (Goering et al. 1990, Ostrom et al. 1997, Tamelander et al. 2009). Given this potential uncertainty in regards to the chosen baseline organism, I chose to avoid assigning definitive trophic levels to organisms where possible but instead assigned relative trophic levels. Should an alternate robust organism of known trophic level and present in all three regions be identified, this

information in combination with discrimination factors may be used to assign distinct trophic levels to the presented biplots. One exception to this avoidance of defining definitive trophic levels, however, is during the fourth chapter where the trophic level or each fish was determined to estimate the relationship between trophic level and body mass. However, in this case the trophic level itself was not as important as the predator-prey mass ratio derived from it, which would not have been affected by the potential variability of the reference species.

Throughout this thesis, efforts were made to try to reduce the potential negative impacts that the beforementioned limitations could potentially have on the research. Despite not having a means to measure many of the parameter estimates, I was able to estimate some of them through alternative means (such as estimation of the fractionation coefficient from the collected stomach content data). While not exact, these values were valuable to study as an alternative of using a generic fractionation coefficient such as those proposed in Post 2002 and Caut et al. (2009). Alternatively, a range of potential values were used based on other local studies or those conducted in comparable ecosystems. This range of values should cover the range of biologically viable estimates for the local marine ecosystems. Although the spatial coverage was confined to the major trenches defined by Rose (1993) and to two field sampling seasons, efforts were made to collect the highest quality of data despite these limitations in the interest of thoroughly describing the observed communities. For example, lengths from each individual of every fish species (or at least 100 when they were particularly abundant) were collected and representative isotope samples taken from every caught species. What these studies lack

in spatial and temporal coverage they make up for in coverage of the analyzed communities. A number of assumptions are made when using stable isotope analysis as a tool. However, by complementing the stable isotope analyses with stomach contents data, the impacts of these limitations were reduced.

Future Directions

Expanded spatial coverage within this region would solidify the results of this thesis. The present research focuses purely on offshore communities. Complementary studies focusing on inshore communities are therefore a logical next step to this research. In addition, the present work is centered on the northeast shelf of Newfoundland and does not consider the southern shelves, the Grand Banks, and the Flemish Cap. The regional focus of this research was initially meant to complement to presently unpublished stable isotope research which was conducted by our lab within these more southerly regions in 2012, at least in regard to the isotope mixing model which was the focus of chapter 3. However, as this complementary research has not been published, comparisons with these regions remains a potential future research direction.

A number of assumptions and estimations were made throughout this dissertation based on optimal available data. The third chapter alone uses a wide variety of published estimates to inform the model including annual primary productivity, catchabilities, trophic efficiencies, fractionation coefficients, and relative trophic level of a reference species (in this case a *Calanus* copepod). To account for uncertainty in some of these measures, I provided a range of viable estimates based on values found in published

literature. Ideally, more precise, localized estimates would be obtained to ensure a more accurate representation of reality. Trophic efficiency, for example, has been documented to vary with size (Barnes et al. 2010) while my results assume a static trophic efficiency resulting from a constant PPMR. The specific numbers may change with estimates that are more precise but the overall trends and conclusions are likely to remain.

In addition to greater spatial coverage, an analysis of temporal variation would further our understanding of the dynamics of these communities. Many of the analyzed species are known to be highly migratory and the fish community composition represented in the spring surveys may differ from that in the fall. Although I do not anticipate that overarching trends would differ substantially between seasons, further analysis would test this hypothesis and indicate how robust our results are for characterizing this region. In addition to differing community composition there is also the potential variation in the diets of representative species. While this study focuses on the spring and winter diets, it is quite likely that the summer and fall diets would vary slightly. Seasonal variation in the baseline isotopic values, as noted earlier, are also likely to vary with season (Goering et al. 1990, Ostrom et al. 1997, Tamelander et al. 2009). Year to year variation is also probable. Not only might we anticipate the diets of these fish species to vary (e.g. Krumsick & Rose 2012) but also some evidence exists of long-term shifts in the δ^{15}N beginning at the base of the foodweb (Sherwood et al. 2011). Continued measures of baseline δ^{15}N would help to monitor these changes and allow for better comparison between years and with other studies.

As mentioned at the beginning of this chapter, many factors will influence marine ecosystem dynamics including current oceanographic regimes and climate change. This thesis sought to describe the biotic factors such as species interactions and fishing impacts but was unable to address these abiotic influences on these fish populations. Climate change, which includes increasing ocean temperatures and ocean acidification, in particular is a recent topic of particular concern (e.g. McGinn 2002, Roessing et al. 2004, Fabry et al. 2008, Belkin 2009, Han et al. 2018). These changes may influence community composition and biodiversity by inducing changes in species' distributions (Perry et al. 2005, Harley et al. 2006, Pörtner & Knust 2007), invasive ability (Stachowicz et al. 2002, Occhipinti-Ambrogi 2007, Canning-Clode et al. 2011), mortality rates (Harvell et al. 2002, Hays et al. 2005, Pershing et al. 2015), sensory ability (Munday et al. 2009, Simpson et al. 2011), and productivity (Lawrence & Soame 2004, Blanchard et al. 2012). The interaction these abiotic changes will have on fish and invertebrate communities remains a clear and pressing issue in light of the climate change and continued studies to promote the understanding of how climate change will influence species interactions and size spectra. Steps in this direction have been implemented using a recent Ecopath model (Tam & Bundy, 2019), but studies such as those presented in this thesis are still necessary for future generations of bioenergetic models.

The material presented in this thesis is designed to help fuel future generations of ecosystem-based management recommendations. The approaches towards this end that are recommended are presented purely from a scientific perspective. Although the science is a key input in determining management, there are undoubtedly numerous other

factors, namely socioeconomic and political concerns that are considered in the context of ecosystem based fisheries management (Haedrich & Hamilton 2000, Schrank 2005, Dudley 2008, Khan & Neis, 2010). For example, while balanced harvesting from a theoretical perspective may be an appealing approach towards recovery, it does not accommodate concerns of usage of extra catch with little to no market value and the amount of benefit for the cost of implementation (Charles et al. 2015, Burgess et al. 2015, Reid et al. 2016). Despite the limitations described in the previous chapter, the presented complications with the implementation of balanced harvesting are not meant to undermine potential usefulness but rather point out challenges which we may hopefully overcome. These challenges include economic concerns, enforcement, and how to even effective implementation (see Burgess et al. 2015, Charles et al. 2016, Garcia et al. 2016, Reid et al. 2016). While it can't be denied that these socioeconomic, political, and technical concerns should have a place in management decisions, it should be reiterated that implementing unsustainable solutions on long-term scales or policies that cause widespread damage to the ecosystem will only result in future problems and stock collapses. Yet if we use caution and an ecosystem approach is taken to also consider populations that may not be of economic importance, there is hope that the presently damaged post-exploitation ecosystem may recover to become the productive region it once was considered.

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Appendices

Appendix 1: Ecosystem survey set details

Table A1: Set details for the CE 2013 trip. Measurements without recorded data are noted by a "-".

Set Number	Region	Gear	Duration (minutes)	Speed (knots)	Date	Depth (m)	Bottom Temp. (ºC)	Weight of Catch (kg)	Number of Lengthed Fish	Targeted (T)/ Non-Targeted (N)
8	Hawke Channel	Campelen 1800	16	3.5	04/29	260	3.5	201.3	149	N
9	Hawke Channel	Campelen 1800	15	3.5	04/30	298	3	304.6	164	N
10	Hawke Channel	Campelen 1800	7	3.5	04/30	459	--	60.0	173	T
11	Hawke Channel	Campelen 1800	15	3.5	04/30	305	3.6	201.5	170	T
12	Notre Dame Channel	Campelen 1800	16	3.5	05/01	369	3.8	1007.8	247	N
13	Notre Dame Channel	Campelen 1800	16	3.5	05/03	347	3.5	126.1	165	T
14	Notre Dame Channel	Campelen 1800	18	3.5	05/03	317	3.2	262.3	296	T
15	Bonavista Corridor	Campelen 1800	16	3.5	05/03	320	3.3	90.0	215	N
16	Bonavista Corridor	Campelen 1800	6	3.5	05/03	378	3.5	72.2	123	T
17	Bonavista Corridor	Campelen 1800	16	3.5	05/03	320	3.6	107.6	53	T
18	Bonavista Corridor	Campelen 1800	16	3.5	05/04	315	--	255.5	237	N
19	Bonavista Corridor	Campelen 1800	16	3.5	05/04	308	4.1	344.4	274	T
20	Bonavista Corridor	Campelen 1800	16	3.5	05/04	302	4.0	1066.1	464	T
21	Bonavista Corridor	Campelen 1800	24	3.5	05/05	340	4.0	995.4	490	N
22	Bonavista Corridor	Campelen 1800	7	3.5	05/05	340	4.0	152.1	203	T
23	Bonavista Corridor	Campelen 1800	7	3.5	05/05	300	4.1	308.6	128	T
24	Bonavista Corridor	Campelen 1800	10	3.5	05/05	302	--	1244.1	415	T
25	Bonavista Corridor	Campelen 1800	6	3.5	05/06	332	3.2	38.6	105	T
26	Bonavista Corridor	Campelen 1800	7	3.5	05/06	335	3.5	887.0	348	T
27	Bonavista Corridor	Campelen 1800	7	3.5	05/06	333	2.8	65.1	190	T
28	Bonavista Corridor	Campelen 1800	5	3.5	05/07	302	4.0	86.6	0	T
29	Bonavista Corridor	Campelen 1800	5	3.5	05/07	308	4.0	189.3	123	T
30	Bonavista Corridor	Campelen 1800	17	3.5	05/08	307	3.6	1391.9	785	T

31	Bonavista Corridor	Campelen 1800	21	3.5	05/08	307	3.3	1076.6	391	N
32	Bonavista Corridor	Campelen 1800	5	3.5	05/09	308	3.8	336.5	89	T
33	Bonavista Corridor	Campelen 1800	4	3.5	05/09	308	3.8	362.1	179	T
34	Bonavista Corridor	Campelen 1800	6	3.5	05/10	319	3.3	390.6	475	T
35	Bonavista Corridor	Campelen 1800	14	3.5	05/10	332	3.2	220.3	127	T
36	Bonavista Corridor	Campelen 1800	5	3.5	05/11	342	3.8	504.7	410	T
37	Bonavista Corridor	Campelen 1800	16	3.5	05/12	339	3.3	241.5	354	N

Table A2: Set details for the CE 2015 trip. Measurements without recorded data are noted by a "-".

Set Number	Region	Gear	Duration (minutes)	Speed (knots)	Date	Depth (m)	Bottom Temperature (ºC)	Number of Isotope Samples	Number of Multi-species Stomachs
1	Bonavista Corridor	Campelen 1800	5	3.5	05/06	280	--	4	17
2	Bonavista Corridor	Campelen 1800	19	3.5	05/07	302	2.8	10	32
3	Bonavista Corridor	Campelen 1800	17	3.5	05/07	307	2.8	9	29
4	Bonavista Corridor	Campelen 1800	7	3.5	05/08	327	3.2	39	28
5	Bonavista Corridor	Campelen 1800	9	3.5	05/08	320	3.1	23	21
6	Bonavista Corridor	Campelen 1800	8	3.5	05/08	420	3.4	22	21
7	Bonavista Corridor	Campelen 1800	6	3.5	05/08	470	3.5	24	20
8	Bonavista Corridor	Campelen 1800	16	3.5	05/09	311	3.1	1	0
9	Bonavista Corridor	Campelen 1800	16	3.5	05/09	316	3.1	26	18
10	Bonavista Corridor	Campelen 1800	7	3.5	05/10	300	2.9	14	4
11	Bonavista Corridor	Campelen 1800	10	3.5	05/11	303	2.6	19	14
12	Bonavista Corridor	Campelen 1800	31	3.5	05/11	275	2.1	9	7
13	Bonavista Corridor	Campelen 1800	6	3.5	05/11	322	2.7	11	5
14	Bonavista Corridor	Campelen 1800	6	3.5	05/11	327	2.7	9	6
15	Bonavista Corridor	Campelen 1800	5	3.5	05/12	344	2.8	18	13
17	Bonavista Corridor	Campelen 1800	18	3.5	05/12	285	3.4	22	7
18	Bonavista Corridor	Campelen 1800	11	3.5	05/13	337	2.6	11	8
19	Bonavista Corridor	Campelen 1800	29	3.5	05/14	270	2.2	14	10
20	Bonavista Corridor	Campelen 1800	5	3.5	05/14	267	2.1	7	3
21	Notre Dame Channel	Campelen 1800	43	3.5	05/14	394	2.7	0	15
22	Notre Dame Channel	Campelen 1800	18	3.5	05/15	405	3.9	0	8
23	Notre Dame Channel	Campelen 1800	10	3.5	05/17	286	2.6	0	2
24	Notre Dame Channel	Campelen 1800	16	3.5	05/18	244	2.4	47	28
25	Notre Dame Channel	Campelen 1800	5	3.5	05/18	250	2.3	6	0
26	Notre Dame Channel	Campelen 1800	14	3.5	05/19	362	2.3	6	0

27	Notre Dame Channel	Campelen 1800	5	3.5	05/19	375	3.1	42	8
28	Hawke Channel	Campelen 1800	6	3.5	05/21	306	3.1	16	0
29	Hawke Channel	Campelen 1800	5	3.5	05/21	279	1.9	11	0
30	Hawke Channel	Campelen 1800	6	3.5	05/21	351	2.3	21	2
31	Hawke Channel	Campelen 1800	6	3.5	05/22	471	3.4	16	55
32	Hawke Channel	Campelen 1800	6	3.5	05/22	313	2.8	22	15
33	Hawke Channel	Campelen 1800	6	3.5	05/23	311	3.3	17	42
34	Hawke Channel	Campelen 1800	6	3.5	05/23	217	0.7	14	16
35	Hawke Channel	Campelen 1800	5	3.5	05/24	402	2.9	29	44
36	Hawke Channel	Campelen 1800	8	3.5	05/24	464	3.0	40	1
37	Hawke Channel	Campelen 1800	1	3.5	05/24	413	3.4	6	11
38	Hawke Channel	Campelen 1800	1	3.5	05/24	406	3.4	17	38
39	Hawke Channel	Campelen 1800	1	3.5	05/24	424	3.6	7	8
40	Hawke Channel	Campelen 1800	5	3.5	05/25	268	--	9	0
41	Hawke Channel	Campelen 1800	11	3.5	05/25	350	3.1	1	1
42	Hawke Channel	Campelen 1800	42	3.5	05/25	336	2.7	4	0
43	Hawke Channel	Campelen 1800	43	3.5	05/25	350	2.7	5	0
44	Hawke Channel	Campelen 1800	44	3.5	05/26	447	3.3	19	23
46	Notre Dame Channel	Mid-Water	Unspecified	3.5	05/28	300	--	14	61
47	Notre Dame Channel	Mid-Water	Unspecified	3.5	05/28	310	--	3	0
48	Notre Dame Channel	Mid-Water	60	3.5	05/28	325	--	27	28
49	Notre Dame Channel	Mid-Water	30	3.5	05/29	310	--	10	23
50	Notre Dame Channel	Mid-Water	30	3.5	05/29	375	--	4	9
51	Notre Dame Channel	Mid-Water	40	3.5	05/29	260	--	1	8
52	Notre Dame Channel	Mid-Water	34	3.5	05/29	260	--	2	0
53	Notre Dame Channel	Mid-Water	40	3.5	05/29	300	--	6	19
54	Notre Dame Channel	Mid-Water	30	3.5	05/29	314	--	5	11

56	Notre Dame Channel	Mid-Water	60	3.5	05/30	312	--	1	0
57	Notre Dame Channel	Mid-Water	60	3.5	05/30	310	--	5	0
58	Notre Dame Channel	Mid-Water	90	3.5	05/30	304	--	5	12

Appendix 2: Carbon and Nitrogen Stable Isotope Data

Table A3. Carbon and nitrogen concentrations and stable isotope values used within this thesis divided by region, length and size category when applicable.

Species	Region	Length (cm)	Size Category	δ^{13}C	δ^{15}N	[C]	[N]
Algae	HC			-24.40	5.21	19.71	4.33
	NDC			-25.75	7.18	15.17	2.83
				-23.51	6.62	11.71	2.41
				-23.96	4.83	10.92	1.94
	BC			-20.84	6.08	32.26	6.48
				-21.28	4.00	28.48	7.97
Alligatorfish	HC	11.2	M	-18.98	13.34	38.85	10.43
		12.2	M	-18.40	14.39	47.47	11.69
		12.5	M	-19.00	14.68	49.34	13.21
		13.3	M	-18.83	14.28	49.36	11.69
		13.9	M	-18.82	14.05	48.41	13.29
		14.0	M	-18.96	13.93	48.79	13.28
		14.7	L	-18.47	14.57	39.15	10.30
		15.5	L	-17.93	14.14	31.87	9.92
		16.3	L	-19.14	14.24	46.04	13.48
	BC	6.7	S	-19.83	13.04	35.71	13.04
		8.2	S	-19.33	13.07	38.39	9.80
		10.3	M	-18.95	13.51	37.51	10.05
		11.2	M	-19.37	13.27	40.03	13.27
		13.6	M	-18.26	13.86	47.66	12.15
		15.5	L	-18.46	14.19	45.75	13.75
		16.5	L	-19.88	14.42	56.19	14.42
		19.4	L	-18.91	13.86	49.46	13.94
American Plaice	HC	13.5	S	-19.38	12.93	47.98	14.75
		19.4	S	-20.43	13.16	46.85	14.58
		19.8	S	-19.75	12.36	48.27	14.78
		20.2	S	-19.28	11.83	48.40	15.03
		23.5	M	-19.79	12.76	46.75	14.33
		25.1	M	-19.02	13.45	51.75	16.12
		26.8	M	-19.01	13.19	47.84	15.03
		27.2	M	-19.62	13.83	46.70	14.41
		28.7	M	-19.36	12.78	48.47	15.11
		30.1	M	-19.31	13.27	48.19	14.89
		31.4	M	-19.77	13.91	44.74	14.12
		33.3	M	-19.69	14.18	46.45	14.62
		34.9	M	-19.28	14.08	48.10	14.73
		36.0	M	-19.34	13.07	46.82	15.02

American Plaice	HC	39.6	L	-18.86	14.30	45.63	14.04
		40.2	L	-19.08	14.00	46.96	14.50
		41.0	L	-19.57	13.41	47.89	15.05
		41.8	L	-19.16	14.04	47.57	14.22
		41.8	L	-19.56	13.68	47.70	14.96
		42.9	L	-19.63	13.29	45.20	14.63
		45.8	L	-19.57	13.71	50.13	12.89
	NDC	14.8	S	-19.42	12.73	47.66	14.71
		16.2	S	-19.22	13.01	46.60	14.26
		17.5	S	-19.59	12.04	47.81	14.63
		18.2	S	-19.28	12.60	47.58	14.65
		20.5	S	-19.37	11.90	47.35	14.53
		22.8	M	-19.20	12.95	45.05	14.02
		23.8	M	-19.77	12.52	46.33	14.42
		25.1	M	-19.83	12.98	48.72	14.84
		28.1	M	-19.12	13.49	47.86	14.84
		29.6	M	-19.25	12.58	47.64	14.81
		30.8	M	-19.50	13.32	48.37	15.08
		31.3	M	-20.27	13.55	45.44	14.09
		31.6	M	-19.12	13.04	46.33	14.58
		32.5	M	-18.74	14.18	47.94	14.97
		33.7	M	-18.98	13.44	47.12	14.58
		35.4	M	-19.46	13.63	45.78	14.15
		35.9	M	-19.42	13.19	46.45	14.43
		38.8	L	-18.83	12.71	47.43	14.87
		39.3	L	-19.20	13.52	46.93	14.66
		43.6	L	-18.57	14.29	48.32	14.98
		46.1	L	-18.48	12.99	48.24	14.63
	BC	12.5	S	-20.11	12.04	47.02	14.20
		13.0	S	-20.02	13.52	45.28	13.95
		14.4	S	-18.33	12.80	47.63	13.74
		16.0	S	-19.75	12.01	47.82	14.59
		17.5	S	-19.58	12.04	47.75	14.33
		19.7	S	-19.96	12.05	47.66	14.62
		21.0	S	-19.64	12.34	47.41	14.69
		26.5	M	-19.92	12.82	48.06	14.81
		26.8	M	-20.43	14.03	48.95	15.08
		27.5	M	-19.59	12.51	46.78	14.54
		28.5	M	-19.83	12.85	47.56	14.59
		29.5	M	-19.69	13.79	48.45	14.93
		30.5	M	-19.85	13.70	50.61	15.48
		31.5	M	-19.74	13.39	47.29	14.65
		38.5	L	-18.26	12.03	47.42	14.38

American Plaice	BC	40.2	L	-18.49	12.62	46.18	14.39
		41.0	L	-18.64	12.25	48.24	14.87
		42.5	L	-19.62	13.16	49.27	14.86
		44.0	L	-19.66	13.53	47.70	14.92
		44.1	L	-20.05	13.68	48.53	13.87
		46.5	L	-18.35	12.53	47.17	14.51
Anemone	HC			-19.91	11.29	42.62	10.60
				-20.74	11.03	37.91	10.10
				-20.72	10.26	36.54	8.92
	NDC			-18.78	13.02	33.72	10.56
				-18.39	12.12	39.69	10.97
				-19.93	11.42	38.63	10.30
				-19.35	11.17	27.11	7.75
	BC			-20.52	10.53	27.90	6.77
				-20.65	10.54	37.54	9.98
Arctic Cod	HC	11.0	S	-20.79	11.70	46.86	13.75
		15.6	M	-20.81	12.51	47.27	14.08
		16.7	L	-21.05	12.21	48.34	14.35
		17.5	L	-20.65	12.49	47.27	14.42
		19.7	L	-20.73	12.24	47.55	14.34
	NDC	8.6	S	-20.99	11.62	45.70	13.66
		9.4	S	-20.74	12.17	48.55	14.72
		9.4	S	-20.91	11.76	47.23	14.04
		9.5	S	-20.87	11.49	48.42	14.39
		9.8	S	-20.82	11.77	45.83	13.64
		9.9	S	-21.13	11.96	48.25	14.15
		10.4	S	-21.28	11.87	46.97	14.04
		10.5	S	-20.93	12.15	45.96	13.86
		10.6	S	-21.18	11.68	47.77	14.30
		10.6	S	-20.81	11.58	45.33	13.87
		10.7	S	-21.11	11.92	48.91	14.79
		10.8	S	-21.03	12.17	47.90	14.66
		10.8	S	-20.95	11.80	47.31	13.84
		10.9	S	-21.17	11.99	47.66	14.20
		10.9	S	-20.92	11.60	46.72	13.95
		11.5	S	-21.15	12.31	47.36	14.34
		12.0	M	-20.99	11.77	46.75	14.06
	BC	7.4	S	-21.44	11.40	47.50	13.98
		7.5	S	-20.93	12.16	47.73	13.99
		8.4	S	-21.27	11.49	46.54	13.81
		8.6	S	-21.60	10.97	46.20	14.11
		8.7	S	-21.21	11.75	46.13	13.80
		9.5	S	-20.91	11.94	48.88	14.68
		9.6	S	-21.32	11.64	46.26	13.69

Arctic Cod	BC	10.0	S	-21.15	11.47	45.47	13.57
		10.0	S	-21.25	11.62	46.38	13.77
		10.3	S	-21.10	11.55	46.39	13.58
		10.5	S	-21.10	11.70	43.49	12.98
		11.0	S	-21.35	12.37	44.49	13.52
		11.1	S	-21.66	12.27	46.55	14.15
		11.2	S	-20.97	11.59	47.29	13.92
		11.4	S	-21.41	12.35	47.69	14.53
		11.5	S	-21.28	11.97	47.58	14.16
		12.0	M	-21.31	11.44	46.31	13.84
Arrow Worm	BC			-22.99	7.61	49.29	8.93
				-21.53	7.72	29.82	8.33
Atlantic Cod	HC	14	S	-20.97	13.07	46.35	13.64
		22	S	-20.44	13.12	47.48	14.50
		24	S	-19.76	13.55	47.05	14.45
		28	S	-19.87	14.83	46.99	14.29
		32	S	-19.46	14.52	47.60	14.68
		35	S	-19.17	13.67	47.12	14.44
		39	S	-19.66	14.66	48.45	14.81
		44	S	-19.55	14.89	46.46	14.12
		50	M	-19.33	14.52	47.20	14.43
		53	M	-19.02	14.92	45.72	14.20
		60	M	-19.25	14.85	46.94	14.60
		64	M	-19.42	14.60	46.73	14.40
		67	M	-18.90	14.54	45.69	14.19
		71	M	-18.96	14.88	50.71	15.85
		76	M	-18.89	15.08	47.64	14.50
		80	L	-18.91	14.82	46.83	14.61
		82	L	-18.65	14.91	45.05	13.96
		84	L	-19.12	14.75	46.18	14.67
		86	L	-18.72	15.01	47.36	14.57
		89	L	-19.43	14.90	45.64	14.24
		104	L	-18.66	16.12	47.08	14.65
	NDC	25	S	-20.59	13.72	46.79	14.13
		29	S	-20.10	14.47	47.48	14.11
		30	S	-19.77	13.91	45.92	14.12
		33	S	-20.43	14.38	48.25	14.50
		38	S	-20.19	14.22	47.43	14.20
		42	S	-19.80	14.14	47.06	14.43
		44	S	-19.78	14.15	47.93	14.75
		46	M	-20.00	13.99	47.86	14.67
		50	M	-20.17	14.47	47.74	14.64
		54	M	-19.43	15.34	41.63	12.75
		59	M	-19.51	14.50	46.31	14.55

Atlantic Cod	NDC	62	M	-19.91	14.53	46.97	14.44
		65	M	-19.22	15.46	47.49	14.60
		69	M	-18.73	15.22	46.69	14.51
		74	M	-19.26	14.78	46.52	14.64
		77	M	-19.20	14.99	44.63	14.48
		81	L	-19.16	15.07	45.84	14.75
		85	L	-19.30	15.27	46.50	14.96
		88	L	-18.59	16.46	45.87	14.16
		91	L	-19.31	15.53	47.31	14.51
	BC	21	S	-20.26	14.79	46.35	13.89
		27	S	-20.60	14.50	47.22	14.61
		29	S	-19.88	14.98	47.06	14.17
		32	S	-20.07	14.10	47.60	14.39
		37	S	-20.01	14.48	47.15	14.31
		41	S	-19.58	14.93	47.19	14.19
		45	S	-19.64	14.70	46.60	14.14
		47	M	-19.40	14.56	47.62	14.45
		52	M	-19.40	14.71	46.94	14.64
		57	M	-18.86	16.86	46.55	14.31
		62	M	-19.47	14.40	47.31	14.67
		67	M	-19.01	15.56	47.98	14.65
		71	M	-19.75	15.43	47.29	14.53
		77	M	-19.33	15.09	47.52	14.81
		80	L	-19.12	14.83	48.27	15.07
		84	L	-18.78	15.44	47.81	14.86
		86	L	-19.14	14.79	46.17	14.10
		89	L	-18.96	16.37	46.74	14.69
		92	L	-19.25	15.69	49.11	15.17
		93	L	-18.81	15.74	47.77	14.61
		98	L	-18.92	16.05	47.09	14.71
Atlantic Herring	HC	31.0	M	-20.87	12.66	52.23	12.37
		32.6	M	-20.52	12.73	53.21	11.14
	NDC	20.3	S	-21.15	11.49	47.95	14.40
		27.1	M	-20.92	11.99	52.31	13.64
		28.7	M	-21.00	11.82	48.50	14.56
		29.4	M	-21.35	12.67	48.63	14.39
		30.8	M	-21.02	11.87	49.36	14.23
		32.0	M	-20.84	12.62	48.48	14.44
		32.2	M	-20.40	12.24	46.10	14.01
		33.5	L	-20.86	12.24	54.10	11.50
		35.2	L	-20.76	12.53	52.44	12.65
	BC	30.0	M	-21.10	12.31	47.56	14.58
		31.8	M	-20.94	12.10	47.08	14.77

Atlantic Herring	BC	32.3	M	-21.10	12.52	52.46	12.68
		32.5	M	-20.70	12.01	47.22	14.53
		36.5	L	-19.95	12.42	50.56	12.42
		37.0	L	-20.63	12.72	52.44	12.72
		37.2	L	-20.85	12.59	54.67	12.59
		38.0	L	-21.07	12.67	54.13	12.67
		38.5	L	-21.36	12.42	53.56	12.42
Atlantic Poacher	HC	12.1	M	-19.07	13.80	49.12	13.69
		14.4	M	-19.42	13.27	49.42	13.66
		22.4	L	-18.90	14.14	57.45	10.29
	BC	6.2	S	-19.27	12.82	37.20	10.71
		10.1	S	-19.25	14.00	48.44	13.38
		10.4	S	-19.15	13.73	45.39	13.05
		10.6	S	-19.25	13.88	43.88	12.24
		15.5	M	-18.77	14.35	52.13	9.88
		16.1	M	-19.37	13.97	50.78	12.90
		19.0	L	-19.16	14.61	48.94	9.90
		20.2	L	-19.31	14.14	50.78	13.03
		20.9	L	-19.62	14.21	48.28	12.99
Basketstar	HC			-14.65	8.89	20.96	2.97
	BC			-15.08	9.00	21.23	2.99
				-14.64	9.91	20.47	2.93
				-13.47	8.73	18.92	2.73
Blue Hake	HC	31.2	M	-20.14	12.38	50.22	14.40
Brachiopod	BC			-10.68	11.20	18.01	3.19
				-7.63	10.87	16.55	2.15
Brittlestar	HC			-10.39	7.03	17.88	2.53
				-11.63	8.30	19.53	2.82
				-10.99	6.61	17.54	2.79
	NDC			-9.71	6.97	17.61	2.16
	BC			-7.96	7.49	14.54	1.49
				-19.39	11.78	44.13	12.17
				-7.84	7.44	15.13	1.48
Capelin	HC	14.9	M	-21.12	11.52	47.72	13.87
		15.6	M	-21.10	12.00	48.21	14.01
		15.8	M	-20.35	11.26	57.54	10.34
		16.6	L	-20.79	11.53	50.58	11.70
		16.7	L	-20.82	11.40	45.42	13.79
		16.9	L	-20.65	12.50	46.30	13.25
		17.0	L	-20.69	12.16	48.25	13.82
		17.3	L	-20.79	11.61	49.20	13.92
	NDC	14.3	M	-20.62	12.02	49.14	13.08
		14.4	M	-21.37	11.26	49.37	12.74
		15.0	M	-21.00	12.14	49.06	13.75

Capelin	NDC	16.0	M	-21.27	11.08	48.42	13.22
		16.7	L	-21.32	11.73	47.74	14.02
		17.5	L	-20.62	12.52	49.15	14.26
		17.9	L	-21.11	11.72	48.31	13.79
		18.1	L	-20.10	12.36	46.63	10.85
		18.8	L	-20.86	12.08	47.67	14.15
	BC	11.0	S	-21.58	12.15	48.31	13.74
		11.6	S	-21.94	11.08	40.04	11.61
		13.6	S	-21.14	12.18	46.77	13.56
		14.5	M	-21.03	11.58	47.13	13.90
		15.5	M	-20.94	11.66	50.01	13.58
		16.4	M	-21.11	11.51	49.11	13.03
		17.0	L	-20.80	12.02	48.59	14.19
		17.3	L	-20.89	11.69	46.96	13.89
		17.7	L	-20.64	11.42	52.03	11.86
Checker Eelpout	HC	10.4	S	-19.82	12.42	46.75	13.84
		15.1	S	-19.78	11.97	45.90	13.73
		19.9	S	-20.00	11.65	49.96	13.17
		21.9	S	-19.26	12.94	48.00	14.59
		26.7	M	-18.83	12.50	48.16	15.07
		30.8	M	-18.86	12.77	47.14	14.56
		33.0	M	-18.50	13.27	48.51	14.43
		38.6	L	-18.70	13.33	46.00	14.24
		42.5	L	-18.60	13.23	47.98	14.68
	BC	11.5	S	-18.75	13.52	44.63	13.38
		16.5	S	-19.25	13.34	48.00	14.76
		19.3	S	-19.19	13.08	43.87	13.45
		23.4	M	-18.91	13.08	47.94	14.95
		28.0	M	-18.54	13.95	48.88	15.27
		28.5	M	-18.13	13.05	47.60	14.59
		32.0	M	-18.76	13.70	48.92	14.46
		37.0	L	-17.97	13.61	48.68	14.76
		45.5	L	-17.76	13.58	46.98	14.46
		47.0	L	-18.03	13.33	47.83	14.81
Clam (*Mya* sp.)	HC			-17.55	11.07	32.86	8.15
				-17.08	10.81	32.60	7.91
				-18.76	12.56	28.84	6.88
	BC			-17.94	13.64	48.44	14.60
				-15.54	11.93	32.81	6.81
Cockle	NDC			-17.95	9.56	32.00	8.80
Copepod (*Calanus* sp.)	HC			-22.15	4.17	38.41	7.56
	NDC			-26.03	6.56	59.61	3.32
				-26.07	5.39	51.06	2.70
				-26.10	6.70	50.23	2.99

Copepod	BC			-18.88	5.89	54.32	6.71
Copepod (non-*Calanus*)	NDC			-26.04	4.87	38.18	2.77
				-25.94	5.25	42.91	3.51
				-26.20	5.68	44.70	3.56
	BC			-21.71	5.56	43.23	9.05
				-21.37	6.32	49.10	8.97
				-20.79	7.19	42.84	7.16
Euphausiid	HC			-20.61	9.86	46.97	10.32
				-19.91	9.14	56.75	8.40
				-21.53	9.47	46.33	10.01
	NDC			-21.05	9.66	45.10	10.72
				-21.17	9.02	46.13	10.65
				-21.61	8.17	47.27	10.19
	BC			-20.85	8.97	49.81	10.36
				-20.55	10.12	45.54	11.46
				-21.44	9.92	45.35	9.94
Four-line Snakeblenny	BC	17.0	M	-18.26	15.21	48.02	14.42
		22.7	M	-17.84	14.80	47.51	14.86
Gammarid	HC			-16.39	11.96	35.10	8.09
	BC			-15.14	11.91	29.91	6.39
				-16.57	11.88	38.16	7.79
				-17.97	5.65	28.40	6.61
Greenland Halibut	HC	11.0	S	-22.01	11.71	45.91	13.80
		13.5	S	-21.72	11.54	46.03	14.30
		17.5	S	-20.86	11.87	46.77	14.21
		19.0	S	-21.07	11.74	49.18	14.10
		21.0	S	-21.13	11.76	45.90	13.15
		22.5	S	-20.74	12.05	48.96	14.36
		25.5	S	-20.46	12.05	48.00	14.38
		26.5	S	-20.51	12.24	50.27	13.71
		29.5	M	-20.39	12.25	48.04	14.26
		31.5	M	-20.41	12.37	48.18	13.02
		33.5	M	-20.19	12.84	50.60	13.07
		35.5	M	-20.34	12.29	53.16	12.25
		37.0	M	-20.28	12.75	53.45	12.83
		40.0	M	-20.10	13.14	56.72	11.27
		43.0	M	-20.30	12.63	54.42	11.84
		45.0	M	-19.80	12.80	54.70	10.11
		46.0	L	-19.30	12.21	59.04	8.99
		47.5	L	-19.9353	12.66	53.55	11.41
		49.5	L	-19.50	12.70	57.16	9.05
		50.0	L	-19.96	12.28	52.51	12.50
		56.0	L	-20.04	12.74	51.63	12.09
	NDC	10.0	S	-22.23	11.68	45.41	13.83
		13.0	S	-22.07	11.63	47.21	14.08

Greenland Halibut	NDC	14.5	S	-21.87	11.20	47.13	14.17
		16.0	S	-22.02	11.39	46.74	13.91
		19.5	S	-21.41	11.12	47.74	14.15
		21.5	S	-20.64	12.23	49.85	12.23
		23.0	S	-21.56	11.53	48.65	13.96
		25.5	S	-21.04	11.82	49.11	11.51
		30.0	M	-21.68	11.60	50.28	13.12
		31.0	M	-20.27	12.85	56.94	10.78
		31.5	M	-20.85	12.74	51.87	13.03
		32.5	M	-20.53	11.98	57.14	10.40
		33.0	M	-19.98	13.23	53.76	11.95
		36.0	M	-21.44	11.73	51.79	12.61
		38.0	M	-20.27	13.02	54.33	10.85
		51.5	L	-20.07	12.82	55.85	10.94
	BC	12.5	S	-21.70	11.77	46.23	13.80
		19.0	S	-21.76	11.98	50.21	12.87
		20.0	S	-21.68	11.75	49.65	13.63
		21.0	S	-21.25	12.70	54.16	15.59
		23.5	S	-21.19	11.46	46.76	13.68
		30.0	M	-20.57	12.38	50.57	13.04
		31.4	M	-20.12	11.96	48.96	13.63
		33.2	M	-20.76	12.32	50.41	13.15
		34.5	M	-20.62	12.42	52.81	12.32
		35.0	M	-20.57	12.59	52.94	12.55
		37.0	M	-19.61	13.22	51.18	11.22
		39.0	M	-20.08	11.95	51.14	12.61
		41.5	M	-19.82	13.39	54.30	11.79
		42.1	M	-20.74	12.91	50.99	12.16
		46.0	L	-20.05	12.60	51.98	11.44
		48.3	L	-20.04	12.39	52.08	12.24
		49.0	L	-19.97	12.84	53.23	11.93
		49.5	L	-19.92	13.45	34.37	7.90
		49.5	L	-20.39	12.87	53.15	12.46
		53.0	L	-20.50	12.65	51.85	13.25
		62.5	L	-19.61	13.57	43.57	9.02
Hookear Sculpin	HC	6.2	M	-18.80	12.72	46.20	13.70
		8.8	M	-18.51	13.13	44.48	13.26
		11.7	M	-18.81	14.06	47.26	14.54
	NDC	3.7	M	-18.36	11.32	39.02	10.60
	BC	5.2	M	-18.42	12.81	41.70	12.55
		7.5	M	-18.43	13.25	43.72	13.25
		10.1	M	-18.29	13.19	47.24	14.40
Hyperiid	HC			-21.42	9.33	39.04	8.49

Hyperiid	NDC			-21.02	8.62	37.88	8.32
				-21.40	8.71	38.50	8.29
				-20.53	8.29	43.78	6.88
				-20.38	8.48	46.64	7.69
	BC			-20.94	8.97	48.16	8.25
				-20.97	9.03	27.74	6.80
				-22.86	8.98	40.93	8.54
				-21.08	9.70	37.48	8.31
Isopod	HC			-18.36	14.83	54.07	11.07
Kelp	HC			-18.13	3.33	37.71	2.06
				-19.82	6.14	26.35	2.11
				-15.63	1.17	36.07	1.62
	NDC			-20.58	6.46	37.13	4.76
				-18.11	2.35	36.67	2.26
				-16.55	3.49	32.30	3.58
	BC			-17.45	4.63	38.42	1.80
				-17.14	5.76	38.32	3.83
Lanternfish (*Benthosema glaciale*)	HC	4.6	M	-20.55	10.89	52.52	12.10
		6.3	M	-20.71	10.42	58.70	10.27
		7.2	M	-20.55	11.16	54.39	10.71
	NDC	4.5	M	-20.24	10.68	58.45	10.66
		6.4	M	-20.26	10.99	57.21	9.88
		8.4	M	-20.18	11.55	56.22	10.82
Lanternfish (*Notoscopelus* sp.)	HC	13.4	S	-20.45	10.88	56.40	11.10
		14.0	S	-20.45	11.08	49.41	12.01
		14.5	S	-20.15	11.44	51.98	13.15
		14.7	M	-20.39	11.61	50.40	11.69
		15.3	M	-20.29	12.00	48.93	13.74
		15.9	L	-20.07	12.56	50.19	13.51
		16.4	L	-20.19	12.12	50.32	13.20
		16.7	L	-19.53	12.00	54.69	12.12
		17.4	L	-20.11	12.34	49.26	13.20
	NDC	12.9	S	-19.18	11.89	54.33	8.16
		14.1	S	-19.29	11.42	59.78	8.88
		14.6	M	-19.78	11.40	57.94	8.76
		14.7	M	-20.61	11.61	56.44	11.83
		14.9	M	-19.78	11.98	56.04	9.65
		15.0	M	-19.00	11.72	59.59	7.95
		15.1	M	-18.97	12.09	61.88	8.96
		15.7	L	-20.06	11.91	59.42	10.36
		16.5	L	-19.74	12.34	57.59	11.53
	BC	13.7	S	-20.37	11.78	55.22	11.97
		14.0	S	-19.86	11.85	57.66	10.16
		14.2	S	-19.68	11.81	58.43	9.30

Lanternfish (*Notoscopelus* sp.)	BC	14.5	S	-20.32	11.24	54.63	12.45
		14.8	M	-19.83	12.18	52.70	12.44
		15.1	M	-20.13	11.81	54.86	12.98
		15.5	M	-19.83	11.91	55.55	10.45
		16.0	L	-20.12	12.05	50.84	12.75
		16.5	L	-19.20	12.15	55.69	9.34
Longfin Hake	BC	11.8	M	-18.84	10.20	42.68	10.62
Marlinspike	HC	28.4	L	-19.73	13.48	46.05	14.31
		30.5	L	-19.64	13.66	48.79	14.64
		30.5	L	-19.74	13.63	48.58	14.99
		34.5	L	-19.66	13.53	47.77	14.80
		35.5	L	-19.44	13.74	48.30	14.96
		38.0	L	-19.38	13.50	47.45	14.80
	BC	8.6	S	-20.63	11.10	48.89	13.05
		17.5	S	-19.45	13.17	47.17	14.15
		24.5	M	-19.12	13.73	48.53	15.04
		28.0	M	-18.99	13.73	48.29	14.91
		28.3	M	-19.45	13.65	48.63	14.17
		28.9	M	-19.18	13.74	46.71	14.64
		29.2	M	-18.70	13.97	48.93	15.03
		35.0	L	-18.81	13.97	48.65	14.95
		38.0	L	-18.66	14.31	47.69	14.75
Moustache Sculpin	HC	9.9	M	-19.86	12.58	47.18	14.32
		12.1	M	-20.39	13.11	48.57	14.00
		15.2	M	-19.08	14.00	48.59	14.83
	NDC	10.6	M	-19.56	14.11	48.33	14.59
		12.7	M	-19.70	14.08	48.67	14.72
		13.7	M	-19.76	14.40	51.74	13.87
	BC	10.0	M	-20.52	13.15	49.27	13.85
		11.2	M	-19.56	13.92	46.43	13.93
		12.3	M	-19.41	13.84	46.05	13.66
Mysid	HC			-22.37	4.62	37.57	8.06
	NDC			-21.93	7.75	38.69	8.98
	BC			-21.57	7.35	41.06	10.04
				-21.49	7.44	37.45	8.84
Nudibranch	HC			-16.60	16.04	31.19	6.74
Ostracod	NDC			-17.23	6.93	53.73	5.34
Polychaete	HC			-19.38	8.17	43.82	9.79
	NDC			-17.93	12.50	38.62	11.71
				-17.21	13.92	44.75	12.00
				-18.17	12.29	34.85	10.25
	BC			-18.51	11.77	37.87	11.30
				-17.13	12.97	34.22	8.18

Polychaete	BC			-17.78	12.19	42.55	11.92
				-16.66	12.72	37.11	8.61
Pycnogonid	HC			-18.70	10.77	42.69	10.81
				-19.97	11.47	41.20	10.54
				-19.96	10.43	37.22	8.79
	BC			-20.46	10.36	22.06	5.96
				-19.51	11.15	41.18	10.34
Redfish	HC	6.0	S	-21.59	11.05	46.63	14.03
		10.1	S	-20.40	11.89	50.11	13.60
		12.0	S	-20.70	12.13	50.17	13.31
		12.7	S	-20.82	12.06	48.23	12.46
		17.0	S	-20.71	11.38	48.54	14.30
		19.0	M	-20.59	12.53	50.07	13.88
		19.7	M	-20.83	11.36	48.13	14.51
		20.0	M	-20.56	11.42	47.34	14.32
		23.6	M	-19.93	12.81	48.83	14.87
		26.1	M	-20.57	12.01	52.14	12.25
		26.9	M	-20.44	12.39	48.65	14.99
		28.7	M	-19.82	12.57	47.65	14.75
		30.0	M	-20.01	12.96	47.53	14.66
		33.6	L	-19.77	12.45	47.15	14.32
		34.6	L	-19.94	12.32	47.53	14.03
		35.5	L	-20.11	12.50	48.25	15.09
		36.9	L	-19.60	13.22	48.59	14.62
		38.8	L	-20.00	12.50	48.37	14.80
		40.7	L	-19.60	13.15	49.79	14.50
		43.6	L	-19.10	13.70	47.96	14.94
		47.8	L	-20.78	11.89	48.25	13.93
	NDC	6.3	S	-21.94	10.63	46.49	13.56
		8.2	S	-21.36	10.84	48.89	13.41
		8.8	S	-20.89	11.34	48.24	13.29
		10.2	S	-20.68	11.93	47.99	13.27
		15.6	S	-20.42	12.45	49.08	15.01
		16.0	S	-20.55	11.94	48.20	14.65
		18.2	S	-20.16	11.95	47.76	13.82
		19.9	M	-20.22	11.63	48.68	14.56
		22.0	M	-20.41	12.07	50.93	14.75
		28.2	M	-20.00	13.02	48.63	14.37
		28.3	M	-20.28	12.07	47.26	14.59
		30.3	M	-19.88	13.00	47.76	14.77
		31.4	M	-20.38	12.14	48.14	14.00
		32.2	M	-20.15	11.78	47.57	14.74
		33.3	L	-20.01	12.72	47.42	14.68
		34.8	L	-19.80	12.19	44.42	14.00

Redfish	NDC	36.3	L	-19.77	12.25	47.97	14.28
		39.5	L	-19.35	13.64	48.05	14.83
		41.7	L	-19.48	13.75	46.37	13.83
		44.1	L	-19.19	14.02	47.96	14.80
		45.4	L	-18.95	14.19	48.54	15.01
	BC	7.0	S	-21.55	10.37	45.85	13.47
		7.0	S	-21.50	10.57	45.34	13.56
		10.3	S	-20.54	11.53	45.81	13.75
		12.5	S	-20.50	11.84	50.52	13.66
		13.2	S	-20.63	11.72	48.41	13.46
		13.5	S	-20.72	11.62	47.45	14.05
		16.5	S	-20.26	12.08	48.09	14.67
		20.0	M	-20.57	11.55	49.09	13.79
		20.1	M	-20.64	11.55	50.05	13.69
		21.3	M	-20.57	11.31	48.39	14.55
		22.5	M	-20.32	12.28	46.31	13.97
		23.5	M	-20.11	12.82	46.59	13.97
		26.0	M	-19.97	11.92	48.29	14.02
		31.5	M	-20.09	12.35	47.90	14.27
		34.0	L	-20.07	11.80	45.83	14.20
		34.5	L	-20.11	12.55	48.05	14.20
		36.0	L	-20.18	12.38	49.99	13.26
		36.0	L	-19.99	11.99	48.28	13.80
		36.0	L	-20.04	12.39	47.39	14.28
		37.8	L	-20.20	12.21	48.28	13.55
		40.4	L	-19.62	13.71	49.09	13.69
		42.0	L	-19.48	13.34	47.70	14.56
Roughhead Grenadier	HC	8.5	S	-20.30	11.74	45.36	12.97
		12.2	S	-19.56	13.43	45.16	13.89
		16.0	S	-19.39	13.91	46.20	13.78
		24.0	M	-19.56	13.88	47.86	14.82
		28.1	M	-19.28	13.97	48.43	15.23
		31.1	M	-19.37	13.63	46.67	14.73
		34.1	L	-18.84	14.19	46.00	14.61
		39.0	L	-18.45	14.21	46.61	14.21
		43.8	L	-19.03	14.28	47.55	14.55
Sea Cucumber	BC			-17.86	9.07	29.45	9.07
				-16.62	8.42	21.15	3.67
				-17.52	9.08	21.49	4.01
				-16.49	7.71	19.91	3.37
Sea Star	HC			-14.44	6.70	21.61	3.19
				-11.68	10.98	17.80	2.23
				-13.35	16.03	28.46	5.75
				-11.78	10.18	17.49	1.96

Sea Star	HC		-10.82	14.64	17.40	1.83
			-15.35	10.04	23.85	3.56
			-13.81	11.86	22.31	4.15
			-13.69	12.18	23.00	4.38
	NDC		-12.37	9.40	19.36	2.84
			-12.71	10.12	18.73	2.56
	BC		-14.70	10.42	17.55	2.68
			-12.51	11.34	20.40	3.28
			-14.63	10.17	19.18	2.59
			-12.84	15.42	28.25	5.51
			-12.83	10.06	19.64	3.13
			-12.65	15.11	29.56	5.69
Sea Urchin	HC		-16.27	7.92	28.76	4.83
			-20.24	8.01	36.92	7.66
			-19.11	5.74	14.30	1.64
Shrimp (*Sabinea sarsii*)	HC		-17.51	13.28	45.67	13.74
			-17.34	14.35	44.56	13.40
			-18.12	12.87	45.79	12.92
	NDC		-17.07	13.19	45.75	14.25
			-17.48	13.33	43.04	13.03
	BC		-17.01	13.34	44.37	13.55
			-16.95	13.94	45.60	14.24
			-17.00	13.36	43.79	13.73
Shrimp (*Pandalus* sp.)	HC		-19.19	10.63	44.32	13.84
			-19.29	10.46	46.87	14.39
			-19.44	10.78	44.93	13.84
			-19.53	10.41	44.04	13.93
			-19.30	11.10	44.03	13.12
			-19.41	11.01	42.56	13.10
			-19.92	10.73	47.56	14.43
			-19.55	10.86	46.28	13.74
			-19.42	10.23	44.49	13.63
	NDC		-19.41	10.68	45.91	13.65
			-19.39	10.70	45.99	14.34
			-19.64	10.70	44.77	13.79
			-19.85	10.26	45.84	14.07
			-19.92	10.82	46.71	14.13
			-19.81	10.78	47.64	14.39
			-19.86	10.04	46.14	14.14
			-19.58	11.16	47.13	14.65
			-20.38	10.05	45.28	13.74
	BC		-18.78	11.84	47.45	14.33
			-18.94	11.10	45.80	14.08
			-18.92	11.73	50.93	15.27

Sipunculid	BC			-22.14	8.51	4.88	1.03
				-21.23	9.00	5.60	1.29
				-21.83	8.87	6.74	1.57
Smooth Skate	HC	30.0	S	-18.53	11.57	42.55	15.04
		31.2	S	-19.23	11.48	44.89	15.62
		33.0	S	-19.16	12.09	43.22	15.19
		35.7	S	-19.30	11.45	3.76	15.78
		37.6	S	-19.25	12.23	45.55	16.04
		41.5	M	-19.31	12.00	45.31	16.82
		51.6	L	-19.03	12.51	45.33	16.65
		52.8	L	-19.02	13.07	43.85	16.40
	BC	56.0	L	-18.64	12.92	44.76	16.69
Snakeblenny	HC	21.7	M	-18.70	13.12	51.12	15.06
	BC	22.3	M	-18.29	14.11	50.87	14.35
		15.1	M	-18.09	13.87	49.39	14.41
Snow Crab	HC	1.0	S	-15.56	10.62	26.09	5.37
		1.8	S	-13.25	9.69	21.25	3.90
		2.4	S	-18.94	10.92	35.59	8.34
		3.1	M	-19.25	11.26	39.95	11.89
		3.4	M	-18.45	11.59	37.97	10.83
		3.7	M	-19.01	11.38	40.75	11.58
		8.1	L	-18.42	11.95	44.55	13.39
		9.0	L	-18.32	12.47	46.11	13.87
		10.3	L	-18.08	12.18	43.89	13.45
	NDC	1.0	S	-16.69	9.24	28.16	6.20
		1.0	S	-14.66	9.01	22.60	4.22
		1.4	S	-14.73	8.43	19.91	3.54
		2.0	S	-12.42	9.26	24.16	4.89
		2.1	S	-13.23	9.60	25.18	5.19
		6.2	M	-17.99	13.17	48.12	14.25
		10.3	L	-17.61	12.14	46.81	14.12
	BC	1.1	S	-14.35	9.01	25.65	5.25
		1.4	S	-14.09	10.40	27.61	5.65
		1.7	S	-13.18	9.26	24.91	5.13
		2.2	S	-16.09	8.93	28.29	5.89
		2.4	S	-17.70	11.06	34.06	8.75
		2.9	S	-18.62	11.09	37.68	10.95
		3.1	M	-18.34	12.02	42.34	12.67
		6.0	M	-20.15	12.21	43.85	27.27
		8.3	L	-17.76	12.36	44.84	13.71
Squid	HC			-20.66	11.04	44.77	12.16
				-19.06	11.49	42.88	12.31
	NDC			-21.55	10.36	45.32	11.93
				-20.47	12.17	47.21	12.73

Squid	NDC			-21.35	11.26	47.80	12.60
	BC			-20.57	11.33	49.72	15.13
				-21.22	11.74	48.41	9.53
				-21.25	10.92	47.15	12.43
Thorny Skate	HC	10.2	S	-18.54	13.94	43.16	14.02
		11.6	S	-18.60	13.46	45.34	13.95
		12.3	S	-18.67	14.26	44.48	13.99
		13.5	S	-18.04	14.75	44.47	14.05
		16.2	S	-18.64	13.01	41.13	14.19
		22.5	S	-18.58	12.50	45.04	16.48
		28.2	S	-18.99	13.08	45.48	16.21
		29.6	S	-18.43	13.00	44.57	16.36
		39.5	M	-19.23	12.55	45.09	16.25
		42.5	M	-18.94	12.71	43.99	16.35
		43.2	M	-18.65	13.67	45.80	16.73
		47.2	M	-18.44	13.12	43.87	15.37
		47.4	M	-18.51	13.74	43.28	16.11
		48.2	M	-18.77	13.40	41.98	15.75
		49.8	M	-19.47	13.19	45.33	15.87
		50.0	M	-18.88	13.62	43.61	16.32
		51.3	M	-18.48	13.52	45.56	16.64
		58.4	L	-19.24	13.26	42.40	14.75
	NDC	31.3	S	-18.87	13.18	43.80	16.38
		42.5	M	-18.36	14.75	46.25	17.02
		51.7	M	-18.56	14.09	44.10	16.51
	BC	13.6	S	-17.75	14.81	43.25	14.06
		21.0	S	-18.10	12.89	49.11	17.40
		21.2	S	-18.34	12.14	41.82	14.89
		25.2	S	-18.58	12.48	42.09	16.67
		27.0	S	-18.61	12.62	44.22	15.93
		30.1	S	-18.65	13.07	44.38	16.44
		32.5	S	-18.72	13.78	44.68	16.32
		34.5	M	-18.91	13.14	44.59	16.24
		36.0	M	-18.69	13.05	44.42	16.86
		37.0	M	-18.68	13.34	44.89	16.09
		39.0	M	-18.51	13.84	42.51	15.37
		44.5	M	-18.73	13.52	45.02	16.79
		45.0	M	-19.16	13.42	44.42	16.86
		51.2	M	-18.58	13.60	43.89	16.28
		54.7	M	-18.61	14.43	44.46	16.76
		55.3	M	-19.00	13.71	44.66	16.87
		57.0	M	-18.84	13.57	41.49	15.21
		57.0	M	-18.03	14.71	44.41	16.49
		60.0	L	-18.39	13.93	44.65	16.90

Thorny Skate	BC	63.0	L	-18.79	14.48	42.46	15.20
		64.0	L	-20.39	12.57	51.92	12.71
Threebeard Rockling	HC	32.9	M	-19.18	13.89	47.18	14.13
	BC	16.5	M	-19.84	13.13	47.53	14.46
		12.9	M	-19.83	13.02	44.61	13.57
		20.5	M	-19.66	13.09	47.71	14.94
		23.7	M	-18.55	14.71	47.76	14.75
		26.9	M	-18.64	14.30	46.91	14.33
Toad Crab	HC	0.7	S	-15.58	9.75	21.61	4.05
		1.3	L	-15.53	10.75	22.84	4.78
		1.8	L	-14.63	8.40	23.92	4.59
	NDC	0.3	S	-18.94	10.30	27.45	5.52
		1.5	L	-15.35	9.41	23.26	4.63
	BC	0.9	M	-16.67	9.49	26.66	4.94
		1.5	L	-15.00	9.55	23.53	4.57
		1.7	L	-16.08	9.52	27.97	6.22
Whelk	HC			-19.52	14.12	43.64	12.20
				-18.61	9.64	44.51	10.66
				-18.18	12.64	43.86	12.45
	BC			-18.01	10.42	46.68	10.75
				-18.22	10.38	43.17	11.75
				-18.89	10.83	46.19	11.16
White Barracudina	HC	24.7	M	-20.44	11.07	49.96	12.77
		26.7	M	-20.12	11.59	58.70	10.48
		28.8	M	-20.15	11.16	58.50	10.42
	NDC	25.4	M	-21.39	8.78	39.58	11.90
		27.0	M	-20.25	12.09	56.65	9.59
		27.8	M	-20.07	11.50	56.84	10.95
	BC	25.0	M	-19.86	11.49	56.47	8.65
		27.0	M	-20.89	10.85	56.02	11.84
		27.2	M	-19.64	11.58	61.71	9.09
		28.6	M	-20.63	10.42	51.58	9.16
Witch Flounder	HC	41.1	L	-16.80	13.18	48.00	14.94
		41.4	L	-17.05	13.22	48.22	14.84
		45.2	L	-17.14	13.16	48.59	14.84
	NDC	26.0	M	-18.27	12.50	48.77	14.72
		40.3	L	-17.21	13.58	46.80	14.43
		45.6	L	-17.12	13.63	47.01	14.57
	BC	8.5	S	-19.72	12.18	42.74	12.52
		14.2	S	-19.28	12.25	47.38	14.20
		14.7	S	-18.60	12.21	46.97	14.12
		17.2	S	-19.06	12.92	47.29	13.37
		22.2	S	-18.48	12.67	47.74	14.06
		22.5	M	-18.52	12.77	47.97	14.73

Witch Flounder	BC	22.7	M	-17.71	12.06	47.34	14.33
		28.0	M	-18.62	14.23	47.87	14.80
		31.7	M	-17.77	13.01	37.26	11.48
		40.2	L	-17.32	13.52	47.15	14.28
		46.0	L	-17.12	13.44	1.27	0.38
		48.0	L	-17.23	13.79	47.58	14.19
		49.9	L	-17.10	13.38	47.60	14.60